



Spatial patterns of demography and genetic processes across the species' range: Null hypotheses for landscape conservation genetics

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Received 10 October 2001; accepted 19 December 2001

Key words: biogeography, effective population size, population variability, spatial patterns

Abstract

Compared with populations near the core of a species' range, edge populations tend to be characterized by low density and high temporal variation. Based on empirical studies quantifying this pattern, we show that effective population size (N_e) could be 2 to 30 times greater near the core of the species' range than near the edge of the range. Hence, the rate of genetic drift may be 2 to 30 times greater near the edge of the range. Despite these strong spatial patterns in N_e , empirical findings indicate that peripheral populations sometimes have less but sometimes have more genetic diversity than core populations. Our analysis indicates that this variation can be explained by uncertainty in spatial patterns of migration rates. Nevertheless, our analysis: (1) provides a framework or null hypothesis for empirically assessing how spatial patterns of migration or selection influence large-scale spatial patterns of genetic diversity, (2) highlights the potential importance of contemporary processes, such as spatial patterns in N_e (cf. historical phenomena, such as range expansion) in the development and maintenance of large-scale spatial patterns in genetic diversity, and (3) provides new context for understanding the conservation value and vulnerability of peripheral populations. The conservation of ecological/evolutionary processes requires understanding large scale spatial patterns of demographic and genetic processes such as that described here.

Introduction

Populations situated near the core of a species' geographic distribution exhibit greater abundance than populations near the periphery. This pattern is predicted by biogeographic models (e.g., Lande 1991; Gyllenberg and Hanski 1992; Lawton 1993; Lawton et al. 1994) and supported by empirical studies (e.g., Hengeveld and Haecck 1982; Brown 1984; Taylor 1986; Hengeveld 1990; Maurer and Villard 1994; Lomolino and Channell 1995; Curnutt et al. 1996). Similarly, populations situated near the core tend to exhibit less temporal variability in abundance (hereafter, variability) than peripheral populations, according to conventional wisdom (Caughley et al. 1988; Scudder 1989; Lesica and Allendorf 1994; Lawton 1995; Channell and Lomolino 2000), biogeographic models (Kendall 1992), and empirical obser-

vations (Lomolino and Channell 1995; Curnutt et al. 1996). Data appropriate for detecting any such pattern are rare for most animal taxa. Consequently, this pattern has been assessed, to our knowledge, for only seven species. Nevertheless, all seven species exhibit the same pattern of greater variability in peripheral populations.

These patterns of abundance and variability are generally thought to be driven by spatial patterns in habitat quality (Scudder 1989; Lawton 1995; Curnutt et al. 1996). More specifically, the patterns may arise because core populations, inhabiting productive habitats, are sources, and peripheral populations inhabiting lower quality habitat, are sinks (Pulliam 1988; see also Holt 1985, 1987). However, not all populations are expected to exhibit these patterns (e.g., Brown 1984). For example, habitat quality across some geographic ranges (e.g., coastal species) may

decline with distance from one edge of the geographic distribution. Future assessments will undoubtedly reveal additional patterns. Nevertheless, all currently available evidence suggests that peripheral populations commonly exist at lower densities and exhibit higher variability.

Thus, biogeographic studies frequently treat these spatial patterns as null hypotheses or fundamental assumptions (e.g., Caughley et al. 1988; Lesica and Allendorf 1994; Lawton 1995; Channell and Lomolino 2000). Taking these spatial patterns for granted, peripheral populations have been portrayed as being of low conservation priority, because they should be more vulnerable to extinction (e.g., Griffith et al. 1989; Pearl 1992; Stevens 1992; Wolf et al. 1996). Relying on the same geographic patterns of demography, others have argued that peripheral populations are of greater conservation priority because of their potentially unique genetic characteristics (e.g., Scudder 1989; Lesica and Allendorf 1995). These contradictory claims indicate that enlightened conservation of species and underlying ecological/evolutionary processes requires understanding large scale spatial patterns of demographic and genetic processes.

With this motivation, we characterize spatial patterns in the potential strength of genetic drift across the geographic distribution of six species of North American grassland birds (Fringillidae). Our characterizations are based on predicting spatial patterns in N_e from documented spatial patterns in abundance and variability, two of the most important predictors of N_e (Vucetich et al. 1997).

Methods & results

Spatial patterns in the strength of genetic drift

The strength of genetic drift is inversely related to a population's effective size (N_e), which is determined largely by a population's abundance and variability (Vucetich et al. 1997). Thus, large-scale spatial patterns in abundance and variability would likely generate important spatial patterns in N_e . The relationship between abundance, variation in abundance, and N_e is approximated by (Crow and Kimura 1970):

$$N_e = N/(1 + CV^2) \quad (1)$$

where N represents average abundance, and CV is the coefficient of variation in abundance over time.

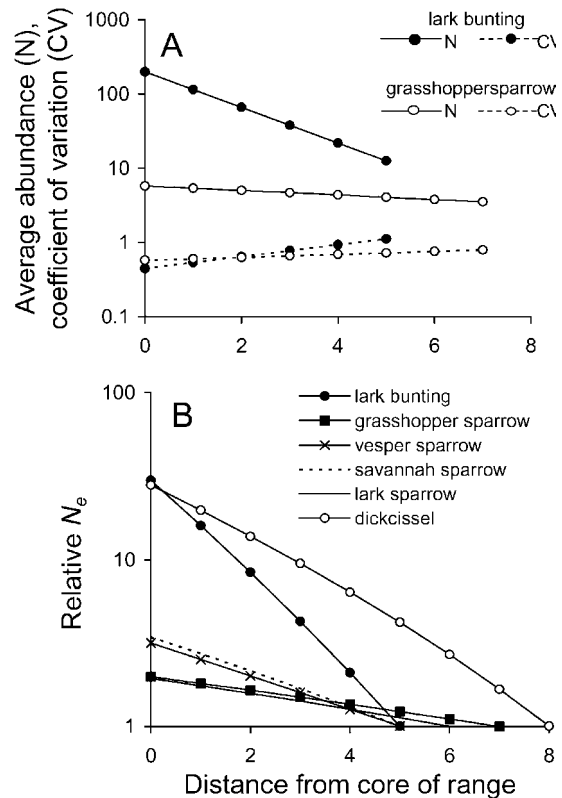


Figure 1. Observed spatial patterns in average abundance (N), temporal fluctuation in abundance (coefficient of variation [CV]), and predicted spatial patterns in effective population size (N_e) over the geographic range of several species of grassland birds. (A) Lines represent regression equations presented in Curnutt et al. (1996). The y-axis is on a log scale and abundance is measured as the number of birds observed on various Breeding Bird Survey routes. Distance from the core refers to the number of degrees latitude-longitude from the core of the species' range. (B) Regression lines from panel (A) are used to calculate N_e (using Eq. 1) over each species' range. Because Figure 1A represents an index of abundance, our interest is limited to the slope of the line (rather than the intercept); therefore, we have rescaled Figure 1B such that $N_e = 1$ at the edge.

Relying on Equation (1) and point-count data (an *index* of abundance) obtained from the North American Breeding Bird Survey (BBS) and analyzed by Curnutt et al. (1996) (Figure 1A), we predicted spatial patterns in N_e across the geographic distribution of six grassland bird species. More precisely, we calculated an *index* of N_e by replacing N and CV (in Equation 1) with the index of abundance and the variation in this index. Because detection probabilities based on the point-count method are unknown, the relationship between observed abundance and absolute abundance is unknown for any of the six species of

interest. Thus, our analysis is based on the plausible assumption that the index of abundance is proportional to actual abundance. Provided this assumption holds, indexed N_e should be proportional to actual N_e . Despite this and other statistical concerns (Sauer et al. 2000; see also Bart et al. 1995), BBS data are useful for characterizing broad patterns such as relative abundance and variability across geographic scales (e.g., Curnutt et al. 1996, detailed information about the BBS can be found at: <http://www.mbr-pwrc.usgs.gov/bbs/bbs.html>).

To characterize variation in N_e across the geographic distribution, we calculated *relative* N_e at various locations across the species range. Relative N_e is the indexed N_e at a specified location divided by the indexed N_e at the periphery. For example, a local population with a relative N_e of 10 would have an effective population size 10 times greater than a local population situated near the periphery. Relative N_e will be unaffected by other predictors of N_e (i.e., sex ratio, degree of generational overlap, and variance in fecundity [Nunney and Elam 1994]), provided they do not vary systematically across space.

For each of the six species examined, the decline in relative N_e (and hence in N_e) with increasing distance from the core is approximately exponential (Figure 1B). For these species N_e is predicted to be 3–300 times greater at the core of the species range than at the edge (Figure 1B).

Spatial patterns in genetic diversity

Spatial patterns in genetic diversity have been observed across the geographic distributions of many species. Such patterns are routinely attributed to historical events such as range expansion (e.g., Highton and Webster 1976; Bellemin et al. 1978; Vaisanen and Lehtasalmi 1984; Sage and Wolff 1986; Cwynar and MacDonald 1987; Descimon and Napolitano 1993; Merila et al. 1996). However, contemporary processes, such as large scale spatial patterns in N_e , may also contribute to the generation and maintenance of patterns in genetic diversity (Templeton et al. 1995; Templeton 1998) (Figure 1).

Here, we assess the potential influence of spatial patterns of N_e on spatial patterns in genetic diversity. Equilibrium genetic diversity for neutral loci is expected to depend on both N_e and m , the (per generation) immigration rate (Futuyma 1986):

$$H = 1 - (4N_e m + 1)^{-1}. \quad (2)$$

The assumptions and application of equation 2 are discussed in Vucetich and Waite (2000) and references therein. Equations (1) and (2) are traditionally used to describe discrete, local populations connected by gene flow. However, we aim to describe local genetic diversity at regular intervals across the entire range of a species. Conveniently, this can be achieved by recognizing that a single, highly connected population extending over a large portion of a species' range can be described with Equations (1) and (2) as several smaller populations connected by appropriately high values of m (see Lande 1992).

Before examining how H (in equation 2) is affected by spatial patterns in N_e , we must select patterns of spatial variation in migration. To consider the full range of possibilities, we assumed that m decreased exponentially, remained constant, or increased exponentially with distance from the core of the species' range. Immigration rates might decline with distance from the core if habitat quality declines with distance from the core and if high habitat quality permits core populations to produce many surplus individuals that become dispersers. However, m might increase with distance from the core if low habitat quality associated with edge populations results in high rates of home range/territory vacancies that are subsequently filled by immigrants. These patterns are plausible if the species' geographic range is much greater than an individual's dispersal ability. Although we expect additional or alternative patterns and mechanisms to occur in nature, the pertinent point is that these three patterns of migration cover a range of possibilities.

Also pertinent is that no empirical data exist on patterns of migration across a species' range, despite many efforts to understand patterns of migration (reviewed in Hanski and Gilpin 1997) and large scale spatial patterns of demography (e.g., Ranta et al. 1997; Turchin and Hanski 1997; Stenseth et al. 1999; Erb et al. 2000). Thus, only a hypothetical treatment of m is permitted. This general level of ignorance strengthens the rationale for our analysis.

For the six species examined, the ratio of N_e at the edge to N_e at the core ($N_{e(edge)}:N_{e(core)}$) ranged from ~ 0.03 (dickcissel) to ~ 0.33 (grasshopper sparrow). Reflecting this range, we examined spatial patterns in H across a species' range for values of $N_{e(edge)}:N_{e(core)}$ ranging from 0.02 to 1.0 (Figure 2). The spatial patterns of H in Figure 2 reflect, in part, the exponential increase of *relative* N_e from 1.0 at the edge to $[N_{e(edge)}:N_{e(core)}]^{-1}$ at the core. The exponential relationship is justified by Figure 1B.

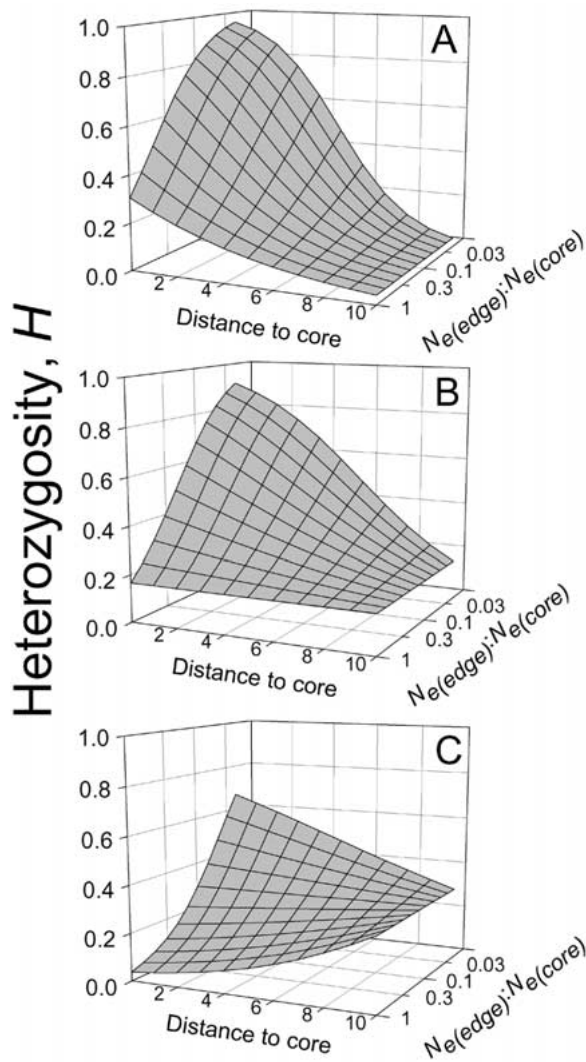


Figure 2. Theoretical spatial patterns in genetic diversity (H , equation 2) as a function of the ratio of effective population size on the edge of a species' range to that at the core ($N_{e(edge)}:N_{e(core)}$) and distance (arbitrary units) from the core of the species' range. These spatial patterns generated by eqs. 1 and 2 are shown for three arbitrary patterns of migration rate (m): (A) exponential decrease with distance from the core (from 0.11 at the core to 0.01 at the edge), (B), constant (0.05) throughout the range, and (C) exponential increase (from 0.01 to 0.11). Note that the x -axis ($N_{e(edge)}:N_{e(core)}$) is on a logarithmic scale.

Where $N_{e(core)}$ is 30 times higher than $N_{e(edge)}$ (i.e., $N_{e(edge)}:N_{e(core)} = 0.03$; lark bunting in Figure 1B), and m is assumed to decrease exponentially with distance from the core of the species' range (Figure 2A), heterozygosity at the core, H_{core} , is 24.2 times higher than heterozygosity at the edge,

H_{edge} (upper right edge of the surface in Figure 2A). However, H_{core} is only 12.2 times higher than H_{edge} for species in which $N_{e(core)}$ is about 3 times higher than $N_{e(edge)}$ (i.e., $N_{e(edge)}:N_{e(core)} = 0.33$; savannah sparrow in Figure 1B). These discrepancies between H_{core} and H_{edge} are attributable to increasing H_{core} with decreasing $N_{e(edge)}:N_{e(core)}$. These patterns contrast with the unrealistic situation where N_e is constant throughout the species' range. Specifically, when $N_{e(edge)}:N_{e(core)} = 1$, H_{core} is only 8 times higher than H_{edge} (lower left edge of the surface in Figure 2A).

Figure 2C shows the predicted patterns in H where m is assumed to increase exponentially with distance from the core. H_{core} is 1.8 times higher than H_{edge} for species in which $N_{e(core)}$ is 30 times higher than $N_{e(edge)}$ (lark bunting; Figure 1B). However, the trend is reversed for species with less pronounced spatial patterns N_e (e.g., savannah sparrow; Figure 1B). In such species, H_{core} is lower than H_{edge} . Figure 2B shows the predicted spatial patterns in H where m is assumed to be constant throughout the species' range. These patterns are intermediate to those described for the cases of increasing m (Figure 2C) and decreasing m (Figure 2A).

Discussion

Some demographic factors that influence effective population size (N_e ; Figure 1) vary systematically throughout a species' range, leading to spatial patterns in genetic diversity (Figure 2). Beyond its value as a predictor of the rate of drift, N_e is a potentially important predictor of fitness (Lande 1995; Lynch 1996) and extinction risk (Frankham and Ralls 1998; Saccheri et al. 1998), and has been a useful tool for defining conservation goals (e.g., Mace and Lande 1991; Allendorf et al. 1997; Nunney 2000). Studies concerned with N_e and its implications should recognize that it varies systematically not only over time (Vucetich and Waite 1998) but also over space (Figure 1). These predicted patterns have implications for better understanding a variety of genetic processes occurring at landscape scales.

For example, contemporary spatial patterns in N_e (Figure 1A) may affect large scale spatial patterns in genetic diversity (Figure 2). Considering that spatial patterns in N_e vary widely among grassland bird species, we speculate that corresponding spatial patterns in genetic diversity are likely to be

highly variable in nature. If spatial patterns in migration are similarly variable, then spatial patterns in genetic diversity may be even more complex and varied among species (Figure 2). Compared with core populations, edge populations may exhibit levels of genetic diversity that fall within a continuum from much lower to much higher. This novel recognition may help explain empirical findings that peripheral populations sometimes have less genetic diversity than do core populations (e.g., Jain et al. 1981; Schnabel and Hamrick 1990) and sometimes not (Tigerstedt 1973; Betancourt et al. 1991; see also Lesica and Allendorf 1995).

The utility of our model of spatial patterns in demography and genetic diversity is unclear. Although it may be appropriate for some species, not all species will have spatial patterns of demography like the grassland bird species of this study (Figure 1), with higher abundance and lower variability nearer the core (see Lomolino and Channell 1995 for examples). In this context, our model provides a useful framework or null hypothesis for empirical assessments of the processes that govern large-scale spatial patterns in neutral genetic diversity (e.g., RAPDs or microsatellites). Additionally, our model provides a foundation for assessing the relative roles drift and selection play in generating spatial patterns of genetic diversity at nonneutral loci, where the strength of selection may also vary across a species' range (e.g., Gockel et al. 2001; see also Montgomery et al. 2000). Finally, advances in understanding large-scale spatial patterns of migration – a fundamental process about which we know very little – might arise from using our model to interpret empirical spatial patterns in diversity at neutral loci.

Biogeographers have been concerned with elucidating the factors that determine the extent of a species' range (in the absence of obvious geographic barriers) and what prevents a species from overcoming those factors and thus expanding its range (Hoffman and Parson 1991; Hoffman and Blows 1994). In cases where edge populations are more inbred (see Figure 2), a stable range limit may reflect the balance between costs of inbreeding depression (Vucetich et al., in review) and benefits of increased evolutionary potential due to the founder-flush phenomenon (Meffert 1999). Although a variety of demographic and genetic factors combine to determine a species' range, our observations are helpful for understanding some of the mechanisms involved.

Spatial patterns in genetic diversity are often, and sometimes uncritically, used to infer past range expansion and other historical processes. Although historical processes undoubtedly affect contemporary patterns of genetic diversity (Templeton et al. 1995), our observations show that contemporary processes (e.g., spatial patterns in the importance of genetic drift) also have the potential to affect spatial patterns (see also Stewart and Excoffier 1996; Strange and Burr 1998). Rather than discriminate the relative roles of historical and contemporary processes, most assessments of spatial patterns in genetic diversity give potentially unjustified primacy to the role of historical processes (e.g., Highton and Webster 1976; Bellemin et al. 1978; Vaisanen and Lehtvaslaiho 1984; Sage and Wolff 1986; Cwynar and MacDonald 1987; Descimon and Napolitano 1993; Merila et al. 1996). Our observations (Figure 1) and the availability of statistical techniques for discriminating the influence of historical versus contemporary processes (Templeton 1998) justify balanced assessments of the factors that generate and maintain spatial patterns in genetic diversity. For example, both contemporary spatial patterns of demography and historical range expansion following the retreat of Pleistocene glaciers may provide a more complete explanation of current patterns of genetic diversity across the geographic range of the red-backed salamander. In this species, genetic diversity is high near the center of the range and low along the northern and southern edges (Highton and Webster 1976). Although Pleistocene glaciation may explain the low genetic diversity of northern populations, it cannot explain the low genetic diversity of southern populations.

To conclude, populations situated nearer the edge of a species' range may be commonly characterized by lower abundance and higher temporal variability in abundance (Figure 1A). Based on these biogeographic patterns, basic population genetics theory predicts that the effective population size will tend to be smaller for edge populations than core populations (Figure 1B). Our calculations suggest that the rate of genetic drift may be 2 to 30 times higher near the edge of a species' range. This spatial pattern is likely to generate corresponding patterns in genetic diversity throughout a species' range (Figure 2). Our analysis suggests that while some edge populations will warrant special attention because they are highly vulnerable to loss of genetic diversity (unless migration rate is high) (Curnutt et al. 1996; Lomolino and Channell 1996; see also Hoffman and Blows 1994), other edge popula-

tions will warrant such attention because they contain high genetic diversity (see also Lesica and Allendorf 1995). Although variable in nature, large-scale, spatial patterns of demography appear to be common among bird species (Curnutt et al. 1996; Linder et al. 2000), and are probably common among all species. Such demographic patterns and their potential impact on genetic processes across large spatial scales (this study) highlight the need for a landscape perspective in conservation efforts aimed at maintaining ecological-evolutionary processes.

Acknowledgments

We thank L. Vucetich and two anonymous referees for insightful discussion and comments on the manuscript. This work was supported by a McIntire-Stennis grant.

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