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Geographical patterns of turnover and nestedness-resultant components of allelic diversity among populations

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Abstract The analysis of geographical patterns in population divergence has always been a powerful way to infer microevolutionary processes involved in population differentiation, and several approaches have been used to investigate such patterns. Most frequently, multivariate spatial patterns of population differentiation are analyzed by computing pairwise genetic distances or F_{ST} (or related statistics, such as ϕ_{ST} from AMOVA), which are then correlated with geographical distances or landscape features. However, when calculating distances, especially based on presence-absence of alleles in local populations, there would be a confounding effect of allelic richness differences in the population differentiation. Moreover, the relative magnitude of these components and their spatial patterns can help identifying microevolutionary processes driving population differentiation. Here we show how recent methodological advances in ecological community analyses that allows partitioning dissimilarity into turnover (turnover) and richness differences, or nestedness-resultant dissimilarity, can be applied to allelic variation data, using an endemic Cerrado tree (*Dipteryx alata*) as a case study. Individuals from 15 local populations were genotyped for eight microsatellite loci, and pairwise dissimilarities were computed based on presence-absence of alleles. The turnover of alleles among populations represented 69 % of variation in dissimilarity, but only the richness difference component shows a clear spatial structure, appearing as a westward decrease of allelic richness. We show that decoupling richness difference and turnover components of allelic variation reveals more clearly how similarity among populations reflects geographical patterns in allelic diversity that can be interpreted in respect to historical range expansion in the species.

Keywords Allelic richness · Autocorrelation · Cerrado · Correlograms · *Dipteryx alata* · Mantel test · Population divergence · Spatial genetic structure

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Introduction

The analysis of geographical patterns in population divergence has always been a powerful way to infer microevolutionary processes involved in population differentiation (Epperson 2003; Rousset 2004). Implicit spatial approaches for the analyses of population differentiation usually start by partitioning genetic variation within and among local populations or subpopulations, which is commonly measured by Wright's F_{ST} and related statistics (such as θ_P from the Analysis of Variance of Allele Frequencies or ϕ_{ST} from AMOVA; see Holsinger and Weir 2009 for a recent review). In a second moment, explicit spatial analyses have been based using several techniques, including multi-variable techniques based on comparison of spatial autocorrelation patterns for various alleles (see Sokal and Oden 1978a, b; Sokal et al. 1997) and many multivariate analyses that evaluate simultaneously several loci and alleles (e.g., Smouse and Peakall 1999; Vekemans and Hardy 2004). For multivariate analyses, it is possible to build synthetic maps from ordination techniques, usually linear Principal Components (Cavalli-Sforza et al. 1994) or, much more

frequently, to evaluate geographical patterns in pairwise genetic distance matrices among populations using Mantel tests (e.g., Sokal 1979; Manly 1985; Sokal et al. 1986, 1991; Rousset 1997).

Pairwise genetic distances used to evaluate geographical patterns of genetic divergence among populations using Mantel tests have been built using several algorithms, depending on which molecular data is used and how they are coded. Very common metrics are Nei's and Roger's genetic distances, or pairwise ϕ_{ST} from AMOVA (or transformations of F_{ST} and related statistics, such as $[F_{ST}/(1 - F_{TS})]$–Rousset 2004) (see Felsenstein 2004 for a review). Thus, calculations of genetic distances and associated parameters for among-population differentiation rely on allele frequencies, but more recently some analyses started using allelic richness or diversity (i.e., based on the presence or absence of alleles in populations) for comparing local populations or samples. For instance, Cabarello and Rodriguez-Ramilo (2010) recently proposed a new metric for evaluating among-population differentiation component, called A_{ST}, analogous to F_{ST}, based on a matrix of presence-absence of alleles in local populations or samples (see also El Mousadik and Petit 1996). When calculating the A_{ST} it is necessary to compute a pairwise matrix of allelic divergence (in which the diagonal is the number of alleles in each population) and, by analogy with F_{ST}, it is possible to computed pairwise A_{ST} (or eventually $A_{ST}/[1-A_{ST}]$).

Pairwise similarity metrics based on presence-absence data are frequently used in ecological analyses (see Legendre and Legendre 1998), in which local ecological communities or assemblages are described by the presence or absence of species (thus, analogous to describing a population by the alleles present or not). However, an important confounding factor when calculating the similarity occurs because of richness difference, and thus eventual the patterns in similarity among local populations (based on allelic richness) or ecological communities (based on species richness) are due to mixed confounded components due to the differential contribution of richness differences and turnover (replacement) along gradients.

The important issue is that different ecological and evolutionary processes generate replacement (i.e., the substitution or turnover of alleles or species in one site by different alleles in other site) and variation in allele richness differences (i.e., the gain or loss of alleles between populations along a gradient, so the variation in one population is nested into the other). Given that sampling problems are avoided or solved by rarefaction techniques, it is important to recognize that two samples can differ in allelic patterns in different ways. Suppose that populations A and B differ by 5 alleles not in common. In a first situation, an among-population component of allele richness can arise because these two populations differ in their alleles, so population A has 5 alleles and population B has 5 other different alleles. This well characterizes a high turnover of alleles between the two populations. However, a similar difference of 5 alleles can be obtained if population A has 10 alleles and population B has a subset of 5 alleles from those alleles found in population A, so a confounding effect of allele richness differences is driving any metrics used to evaluate divergence among populations based on alleles. This second example indicates that genetic patterns in population B are totally nested within population A. Understanding these two situations is critical for a correct interpretation of processes underlying population differentiation and is also important for conservation decisions.

Although it is easy to recognize the extreme situations presented in the hypothetical example above, it is clear that, when calculating population differentiation using allele presence-absence data with lots of populations and alleles, the two components will be not easy to decouple. This problem was recently recognized and is being widely discussed in ecological research in the context of geographical patterns in β-diversity (Baselga 2010, 2012; Carvalho et al. 2012; Almeida-Neto et al. 2012; Dobrovolski et al. 2012). Despite some methodological discussions, the solution to this "problem" is to decouple diversity using different metrics and interpret then separately.

Here we propose the application of the approach developed by Baselga (2010; see also Carvalho et al. 2012) to evaluate patterns in allelic diversity among populations, called here β-genetic diversity (just to make easier the comparison with ecological literature). The basic idea is to decouple allelic difference among local populations into allelic richness differences (and nestedness-resultant) and allelic turnover components, and evaluate the geographical patterns in genetic similarity of each of these components using spatial analyses. We show how transference of new approaches between ecology and population genetics can provide new tools that may improve our understanding the processes underlying spatial variation in diversity (Diniz-Filho and Bini 2011).

To exemplify the application of the partitioning approach to allelic diversity data, we used microsatellite data from 15 local populations of "Baru" tree (*Dipteryx allata*) in Brazilian Cerrado. The species is endemics to the biome, but it is widely distributed in the Cerrado, occurring in eutrophic and drained soils of seasonal savannas. Previous studies showed a significant amount of spatial genetic differentiation among and within local populations (Collevatti et al. 2010) and broad-scale geographical structure in the species is apparently associated with patterns of habitat fragmentation in the Cerrado (Soares et al. 2008) and historical patterns of range shift after the last glacial maximum (Collevatti et al. in review).

Methods

Genetic data

Genetic data for *D. alata* consisted of microsatellite markers analyzed for 15 local populations widely distributed throughout species' geographical range, for which a 480 individual trees (32 in each local population) were genotyped for eight microsatellite loci (see Soares et al. 2012; Diniz-Filho et al. 2012a for methodological details). This is a subsample of a larger dataset in which sample sizes within each locality ranged from 12 to 32, but to avoid sampling and rarefaction problems when calculating allelic richness patterns and creating more difficult to demonstrate the partition between richness and turnover components of allelic diversity, we restricted our analyses to 15 local populations in which 32 individuals analyzed. These 15 populations are not spatially biased in respect to all local populations sampled, so they must be representative of the spatial processes driving population divergence.

Pairwise allelic divergence between local populations

We calculated pairwise matrices of allelic divergence among the 15 populations using the metrics proposed by Baselga (2010) and Carvalho et al. (2012). The details of computation and derivation of the formulae used for each metrics can be found in these original papers, and only a brief description is given below.

All metrics used for dissimilarity based on 0/1 data between two populations, say 1 and 2, start by the well-know computation of counts of a (number of alleles common to both populations), b (number of alleles exclusive of population 1), c (number of alleles exclusive of population 2) and d (alleles not found in both populations) (see Legendre and Legendre 1998). Several metrics for evaluation differentiation between pairs of populations are available for this kind of data, and according to Baselga's (2010) approach, the overall β-diversity can be computed by Sorensen's dissimilarity index, given by

$$\beta_{sor} = (b + c)/2a + b + c$$

which can be additively partitioned into turnover (β_{sim}) and nestedness-resulting dissimilarity (β_{sne}) components as

$$\beta_{sor} = \beta_{sim} + \beta_{sne}$$

where

$$\beta_{sim} = \min(b, c)/a + \min(b, c)$$

and

$$\beta_{sne} = [(b - c)/(a + b + c)] * [a/a + \min(b, c)]$$

These quantities and indices are expressed here as dissimilarities to better match the notion of diversity (i.e., larger numbers expressing more diversity), and not as similarities. So, β_{sim} express turnover or replacement of alleles between the two local populations, whereas β_{sne} is better viewed as a proportion of allelic richness difference, expressing the nestedness-resultant component of the Sorensen dissimilarity. The relative importance of turnover component for the overall similarity among populations can be thus obtained by $T(\%) = (\beta_{sim}/\beta_{sor}) * 100$.

Almeida-Neto et al. (2012), among other things, criticized the use of the term "nestedness" in this context mainly because other more specific measurements have been proposed and widely tested in a different context (e.g., Almeida-Neto et al. 2008). Carvalho et al. (2012) also criticized the metrics used by Baselga's (2010; but see Baselga 2012) and pointed out that β_{sim} overestimates the turnover component, and proposed different metrics for doing the partition.

For comparison, we calculate pairwise similarity and the overall population differentiation A_{ST}, as proposed by Cabarello and Rodriguez-Ramilo (2010), to perform an initial evaluation of the relative partition of allelic variation within and among local populations. We used Mantel test and correlograms (see below) to correlate pairwise allelic difference with β-genetic diversity estimated using Baselga's (2010). We also computed metrics proposed by Carvalho's et al. (2012), but they generate quite similar results (i.e., matrix correlations between total dissimilarity for Jaccard and Sorensen equals to 0.998; $P \ll 0.01$, and higher than 0.96 ($P \ll 0.01$) for all other components) and only those based on Baselga's (2010, 2012) equations presented above were reported below.

Spatial patterns of population divergence

The spatial patterns in β-genetic diversity and its components, calculated using the formulae described above, were initially analyzed by a Mantel test (e.g., Manly 1985, 1997) between the pairwise matrices of β-genetic diversity and the geographic distance among populations. We also obtained the multivariate correlograms by creating five binary connectivity matrices at increasingly geographical distances among local populations (Oden and Sokal 1986; Borcard and Legendre 2012).

Principal Coordinate Analyses (PCoA; see Legendre and Legendre 1998) were also used to describe patterns of among population variation in these dissimilarity matrices and the first principal coordinate of each population was mapped and related to latitude and longitude to allow a visual inspection of geographical variation patterns. Regressing the first principal coordinate against latitude

and longitude is actually a spatial trend analysis called Trend Surface Analysis (TSA). However, this analysis only captures broad-scale trends (linear, in this case) and other techniques are available today to better describe more complex spatial structures at distinct geographical scales. We used here Moran's Eigenvector Mapping (MEM; see Dray et al. 2006; Griffith and Peres-Neto 2006; Peres-Neto and Legendre 2010) to describe patterns in the response variable, i.e., the first principal coordinates of β_{sor}, β_{sim} and β_{sne}. MEM and related techniques basically starts by an eigenanalysis of transformed geographical distance matrices, and eigenvectors represent spatial relationships among local populations at distinct spatial scales (proportional to the eigenvalues). These eigenvectors are then used to model variation in the response variable (see Diniz-Filho et al. 2009 for application of spatial regression techniques to genetic data).

β-genetic diversity indices were computed using a Q-BASIC program written for this paper, whereas Mantel tests, correlograms, PCoA and MEMs were performed using SAM 4.0 (Rangel et al. 2006, 2010).

Results

There is a significant differentiation among local populations based on allelic presence-absence data, and A_{ST} reveals that 21.3 % of the variation in alleles occurs among local populations. Mean number of alleles per population was equal to 22.7 across all loci, with mean pairwise differences equal to 5.87 alleles (see also Diniz-Filho et al. 2012a for detailed genetic statistics for the species).

The matrix correlation between β_{sor} and Cabarello and Rodriguez-Ramilo (2010) pairwise differences in allelic divergence was $r = 0.885$ ($P \ll 0.001$), indicating that metrics usually applied to ecological data are indeed measuring allelic differences measured in the way more familiar to population geneticists.

The mean parwise dissimilarity among local populations was equal to 0.276, with turnover component (β_{sim}) expressing 68.9 % of the dissimilarity. The mean nestedness-resultant dissimilarity component (expressing allelic richness variation) was equal to 0.086, thus representing about 31 % of the total dissimilarity (in Carvalho et al.'s 2012 approach the proportion of turnover component was again quite similar but slightly lower, equal to 63.9 %).

However, the most interesting issue is that overall Mantel test reveals that, although a significant spatial structure of allelic turnover exists according to overall dissimilarity β_{sor} ($r = 0.352$; $P = 0.002$ for Sorensen's complement), only the allelic richness differentiation component of this dissimilarity is spatially structured ($r = 0.349$; $P < 0.002$; the Mantel's r for the turnover component was equal to $r = 0.047$; $P = 0.872$). Mantel correlograms provide similar results and shows clinal decrease of autocorrelation up to 450 km, stabilizing at the last distance class for β_{sor}, β_{sne}, but not for β_{sim} (Fig. 1). The spatial for β_{sne} is slightly stronger than for β_{sor}, with significant Mantel's r in the second distance class.

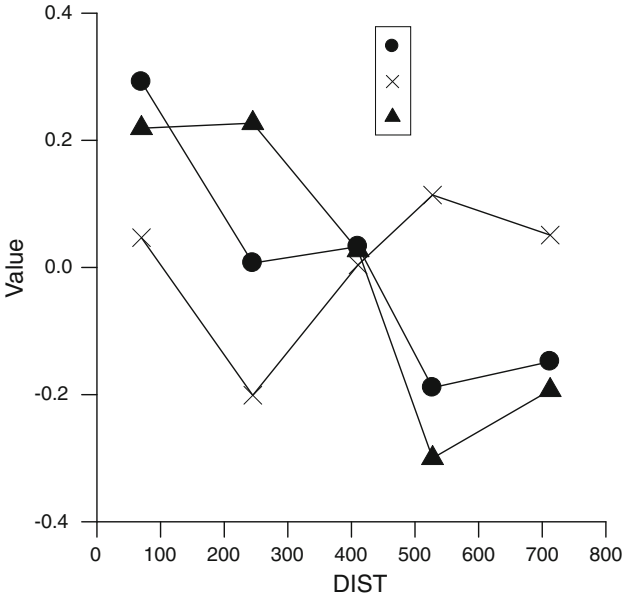

Fig. 1 Mantel correlograms for overall allelic dissimilarity among *D. alata* local populations in Brazilian Cerrado estimated by the complement of Sorensen coefficient (β_{sor}) (*circles*), and for the partition of this overall dissimilarity into replacement (β_{sim}, *crosses*) and richness (β_{sne}, *triangles*)

The spatial patterns in the first principal coordinates extracted from β_{sor}, β_{sim} and β_{sne} support the conclusions from Mantel test and allow a better analysis of trends (Table 1). Supporting the interpretations of partitioning approach, the first principal coordinate of β_{sne} is strongly correlated with allele richness across local populations ($r = 0.995$). For both TSA and MEM, there is only a spatial pattern for first principal coordinate of β_{sne}, with R^2 equal to 0.607 and 0.792 for TSA and MEM, respectively. The TSA allows seeing that this is spatial pattern is actually characterized by a longitudinal linear trend (Fig. 2).

Table 1 Coefficients of determination (R^2) from linear Trend Surface Analysis (*TSA*) and Moran's Eigenvector Mapping (*MEM*) for the first principal coordinate extracted from β_{sor}, β_{sim} and β_{sne}

Matrix/method	TSA	MEM
β_{sor}	0.023*ns*	0.208*ns*
β_{sim}	0.177*ns*	0.428*ns*
β_{sne}	0.607**	0.722**

ns not significant ($P > 0.05$); ** $P < 0.01$

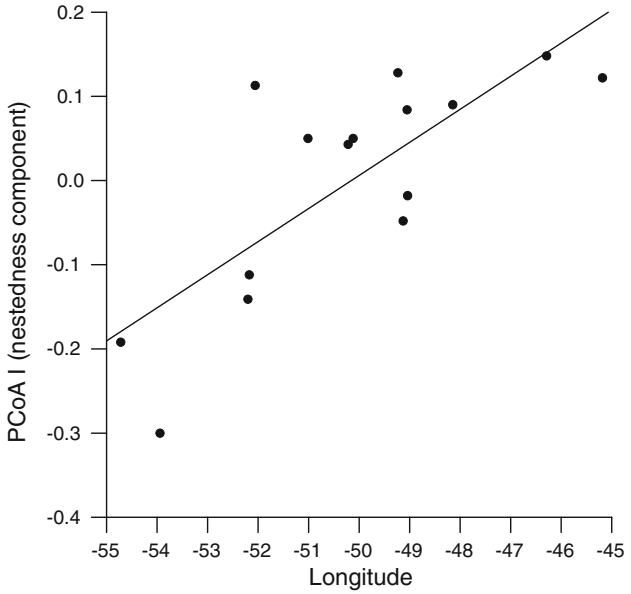

Fig. 2 Longitudinal pattern in the first principal coordinate extracted from the richness (β_{sne}) dissimilarity among populations of *D. alata* ($R^2 = 0.607$)

Discussion

Our analysis reveals that there is a significant population difference in allelic diversity ($A_{ST} = 21.3$ %), and this result is qualitatively similar to AMOVA ϕ_{ST} (0.267) based on the variation in allele frequencies among populations (Collevatti et al. in review). There is also an overall spatial pattern in this differentiation according to Mantel test and Mantel correlograms, so closer local populations in geographical space tend to be more similar in terms of allelic variation. However, the partition of dissimilarity of allelic variation among populations, using the approaches recently proposed by Baselga (2010, 2012) reveals a more complex pattern and more information can be extracted from this data.

The partition of total allelic dissimilarity (β_{sor}, the complement of Sorensen's coefficient—see Legendre and Legendre 1998) into turnover and richness difference (nestedness-resultant) components shows that a relatively high proportion of this difference (ca. 69 %) is due to differences in composition of alleles (turnover), independent of number of alleles, among populations (notice that, because sample sizes in local populations are the same, this is not an artifact). However, spatial analyses show that geographical structure observed in overall dissimilarity is not in this main turnover component, but rather in the allele richness variation component, expressing nestedness-resultant dissimilarity. This spatial pattern appears mainly as a longitudinal gradient in which there is a westward decrease in allelic richness (see Fig. 2).

There are interesting implications for these finding, in terms of the methods applied here and for the understanding of the processes underlying spatial patterns in genetic divergence among *D. alata* populations. Geographic structure in allelic richness has important implications for understanding evolutionary processes and for conservation applications, but there is also an important methodological issue when comparing populations or samples. Gradients in allele frequency are usually hard to detect because the interplay between selection, drift (surfing) and environmental gradients is not clear cut and due to complexity of demographic expansion (see Excoffier et al. 2009 for a review). During demographic expansion, allele surfing may induce the structuring of newly colonized areas into distinct sectors (Excoffier and Ray 2008). In addition, the observation of expected patterns of gradients in spatially expanding populations depends on the levels of recent and past gene flow between subpopulations. Also, gradients in allele frequency are usually detectable for high-frequency alleles, which are more likely to surf, and rarely observed for low-frequency alleles. The difficulties in analyzing allele frequencies can be partially overcome if allelic patterns are directly analyzed and similarity among populations due to different components of allele richness differences and turnover along environmental or geographical gradients.

Thus, coupling our findings with other evidence allow to think that the strong cline in allele richness observed in our analyses can be explained by a process of range expansion after the Last Glacial Maximum (LGM; Excoffier and Ray 2008; Excoffier et al. 2009). As recently discussed by Collevatti et al. (in review), hindcasting paleodistribution of *D. alata* using niche modeling (species distribution modeling—see Nogués-Bravo 2009) showed a strong reduction in habitat suitability for the species in Central Brazil during the LGM, followed by expansion of suitable areas after ~6,000 year BP. This climate change may have caused population shrinking in most part of geographical distribution followed by expansion after the climate became moister and warmer, at ~6,000–5,000 year BP, as a result of migration of populations as though tracking the climate changing. Although the repeated cycles of range shift due to glaciation may have caused complex patterns of genetic similarity among populations, but partitioning allele richness difference and turnover components of divergence among populations more clearly reveals the clines due to demographic expansion in the past.

However, it is important to realize that, although clines coherent with range expansions since LGM were observed in allelic richness and first principal coordinate of β_{sne} matrix, the overall nestedness-resultant component explains only about 31 % of the total variation in allelic dissimilarity. This supports the overall idea that other mechanisms are involved in population differentiation. For instance, replacement or turnover of genetic diversity is expected to occur at relatively

small geographical distances, because of limited dispersal, and this is actually the basis for spatial explicit models in population genetics, including isolation-by-distance (IBD) and stepping-stone models. Under these models, an exponential-like decrease of genetic similarity with increasingly geographical distances is expected, and these patterns have been continuously analyzed using Mantel tests and spatial autocorrelation analysis (Sokal and Wartenberg 1983; Barbujani 1987; Epperson 1995, 1996; Hardy and Vekemans 1999; Vekemans and Hardy 2004; see also Soininen et al. 2007; Diniz-Filho et al. 2012b).

However, no spatial patterns in turnover component are observed in our analysis. This could be explained by sampling problems, if the distances between closer points are larger than needed to allow dispersion and origination of spatial structure. This is unlike in our analysis, because the 15 local populations are a random spatial sample of the entire dataset. Thus, other interesting explanation is that the effects of IBD and turnover were recent (in time), so it is not observable at the levels of alleles (because there was no time for fixation of all alleles in distinct places and combinations), but rather in terms of frequencies. Indeed, an analysis of spatial patterns based on allele frequencies showed a strong correlation between pairwise ϕ_{ST} from AMOVA and geographical distances ($r = 0.494$; $P < 0.001$), independent of allelic richness. Soares et al. (2008) also found some discontinuities among local populations that could be attributed to habitat fragmentation, but this was not also observed here (i.e., there are no broad-scale differences between populations as well).

In conclusion, our analysis reinforce that partition of β-genetic diversity into components may be a quite useful analytical strategy for better understanding the differences among local populations in terms of allelic variation. We believe that the present analysis also highlights how sharing new approaches and methods between different fields, such as community ecology and population genetics, can provide significant improvements to our understanding of processes underlying diversity patterns (Diniz-Filho and Bini 2011). The lack of spatial patterns in the turnover component is probably due to small time scale of evolutionary processes potentially driving such spatial patterns (such as IBD). The analysis of overall dissimilarity may hide some important patterns, so decoupling nestedness-resultant and turnover components allows a clear view of how similarity among populations is reflecting geographical clinal patterns in allelic richness that can be interpreted in respect to historical range expansion in the species.

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