

Holocene re-colonisation, central-marginal-distribution and habitat specialisation shape population genetic patterns within an Atlantic European grass species

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Background

Population genetic patterns are often studied with a focus on either the phylogeographic history of a species, range centre-margin effects, or ecological species characteristics, but rarely on combined effects. Here, we present an integrative population genetic study of *Corynephorus canescens* (grey hair-grass), a short-lived Poacean species, distributed throughout Atlantic regions of Western and Central Europe, but not in the two other classical European glacial refuge regions (Appenine and Balkan Peninsulas). Its specialisation on scattered and disturbance-dependent sandy habitats but high gene flow potential imply strong meta-population dynamics.

Due to these ecological and biogeographical characteristics we hypothesised to find the following patterns: (i) SW European glacial refugia and post-glacial expansion to the NE; (ii) decreasing genetic diversity from central to marginal populations; and (iii) interacting effects of high gene flow and disturbance-driven genetic drift.

Methods

Forty-nine populations (326 individuals) were analysed using AFLP (Amplified Fragment Length Polymorphisms) with three primer combinations (137 polymorphic loci). Gene pool differentiation was investigated with three non-hierarchical genetic clustering methods: *Structure*, *DAPC* and *Geneland*. Genetic variation among (F_{ST}) and within (band richness, Br) populations was assessed and isolation-by-distance was tested with a Mantel test between matrices of population pairwise geographic distances and linearised F_{ST} values.

To include range marginality in a regression study of genetic diversity patterns within the distribution range of *C. canescens*, and to account for its highly scattered distribution, we tested three numeric marginality indices:

Areal Marginality (M_r) as the percentage area outside (A_{out}) the distribution range of circular buffers constructed around each location. Three radii (r) were tested (50 km, 100 km, 200 km):

$$M_r = \frac{A_{out}}{\pi r^2} \cdot 100$$

Minimum Distance Marginality (M_{min}) as the minimum log distance (d_{min}) of a location to the range boundary, normalised by dividing absolute distances by the maximum possible minimum distance (d_{maxmin}) within the distribution range:

$$M_{min} = 1 - \frac{\log d_{min}}{\log d_{maxmin}}$$

Average Distance Marginality (M_{av}) as the average log distance (d) of a location to the range boundary in multiple (n) geographic directions, normalised to the maximum possible average distance of any given location within the distribution range (d_{maxav}):

$$M_{av} = 1 - \log \frac{\sum_{i=1}^n d_{(i-360^\circ/n)}}{n} / \log d_{maxav}$$

Results & Discussion

Species history: The three cluster analyses yielded largely congruent results with four (*Structure*) or five (*k-means/DAPC*, *Geneland*) differentiated gene pools (Fig. 1, Tab. 1), indicating gene flow barriers, sequential effects of genetic drift (founder effects), gene surfing and potentially different selection pressures along post-glacial re-colonisation routes.

Clear associations between N German and S German individuals, as well as between Eastern European and Atlantic Coast individuals were observable (Fig. 2) with the Portuguese plants making up the most differentiated gene pool. Genetic diversity was highest in populations on the Iberian Peninsula and along the Atlantic Coast, and population differentiation was also highest within the Iberian gene pool. A significant diversity decrease from the SW to the NE of Europe ($Br \sim$ longitude: adj. $R^2 = 0.268$, $P < 0.001$; $Br \sim$ latitude: adj. $R^2 = 0.197$, $P < 0.001$) was observable, a common pattern of stepping stone-like range expansions (which is characteristic for species with narrow habitat requirements like *C. canescens*).

These genetic structures suggests that *C. canescens* persisted in SW Europe during the last glacial maximum and that re-colonisation took place from these refugia into E and NE regions of Europe during Holocene climate warming. However, the French Atlantic coast and S Germany could not be definitely ruled out as additional refugia.

Marginality and population structure: In simple linear regression analyses, genetic diversity Br was weakly related to marginality indices M_{r50} (adj. $R^2 = 0.087$, $P = 0.022$), M_{r200} (adj. $R^2 = 0.090$, $P = 0.021$) and M_{av} (adj. $R^2 = 0.092$, $P = 0.019$), and more strongly to M_{r100} (adj. $R^2 = 0.127$, $P = 0.007$) and M_{min} (adj. $R^2 = 0.127$, $P = 0.007$). By including longitude, latitude and marginality M_{min} and their interactions as predictors of genetic diversity Br in a multiple linear regression, the model power improved significantly (adj. $R^2 = 0.424$, $P < 0.001$, all variables and interactions significant).

We found moderate differentiation among populations ($F_{ST} = 0.136$, and $F_{ST} = 0.105$ among gene pools) and a pattern of isolation-by-distance (Mantel's $R = 0.574$, $P = 0.0001$). This indicates a gene flow drift equilibrium within *C. canescens*, probably due to its restriction to scattered and dynamic habitats and limited dispersal distances, confirming the meta-population idea for this species.

Table 1. List of inferred gene pools from *Geneland* results with mean values \pm standard deviation of descriptive parameters over assigned populations and population differentiation (F_{ST}) within gene pools, respectively. H_j = Nei's gene diversity; Br = Band richness, $PLP_{5\%}$ = Proportion of polymorphic loci without alleles of frequencies lower than 5%. Equal letters behind mean values for H_j and Br indicate homogeneous groups as detected by Tukey's post hoc test subsequent to significant results of an ANOVA (H_j : $F = 6.544$, $p = 0.0003$, Br : $F = 8.214$, $p = 0.0005$) based on gene pools as grouping factors. ANOVA on $PLP_{5\%}$ revealed no significant differences.

inferred gene pool	populations assigned (No.)	H_j	Br	$PLP_{5\%}$	No. private alleles	marginality M_{min}	F_{ST} within gene pool
Iberian Peninsula	1 - 5	0.278 a \pm 0.017	1.426 a \pm 0.028	0.480 \pm 0.058	0.4 \pm 0.5	0.14 \pm 0.04	0.1128
Coastal Areas	6 - 15, 28, 32	0.279 a \pm 0.012	1.409 a \pm 0.033	0.486 \pm 0.077	0 \pm 0	0.33 \pm 0.23	0.0693
Northern Germany	16 - 21, 24 - 27, 29 - 31	0.241 b \pm 0.022	1.336 b \pm 0.044	0.453 \pm 0.054	0 \pm 0	0.33 \pm 0.19	0.0808
Southern Germany	22 - 23, 33 - 43	0.249 ab \pm 0.028	1.348 b \pm 0.050	0.456 \pm 0.068	0 \pm 0	0.55 \pm 0.06	0.0644
Eastern Europe	44 - 49	0.240 ab \pm 0.032	1.336 b \pm 0.054	0.424 \pm 0.059	0 \pm 0	0.65 \pm 0.09	0.0745

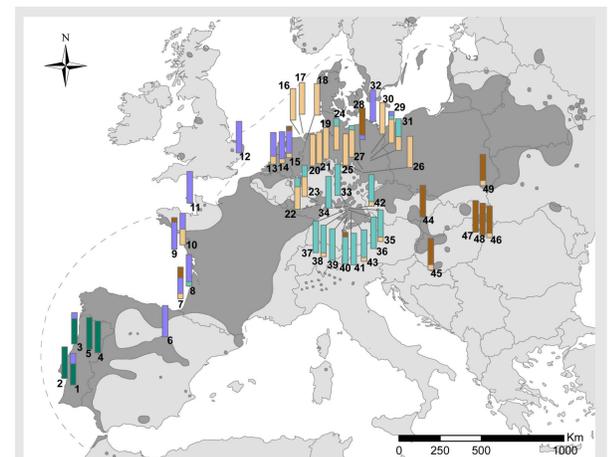


Fig. 1. Distribution range of *C. canescens* (dark grey shading) and sampled populations. Bars represent the portions of individual assignments to the 5 clusters found in the k-means cluster analysis implemented in the DAPC. Colours of the clusters correspond with colouring of points in the DAPC ordination plots (Fig. 2). Dashed lines represent the assumed climatic borders off the coast following Hegi & Conert (1998).

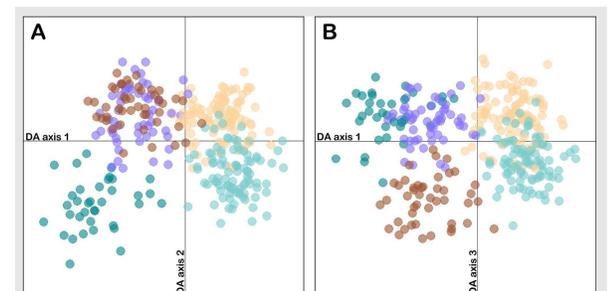


Fig. 2. Ordination plots from the Discriminant Analysis of Principal Components (DAPC) corresponding to Fig. 1. The first two (A) and the first and third (B) axes of discriminant functions are shown. Each point represents one individual distributed along the two linear discriminants, respectively, 13 principal components were retained to get adequate discrimination of clusters, based on a-score optimisation.

Conclusion

- Our study emphasises the need for studying the effects species (re –)colonisation histories and range centre – margin analyses jointly and to consider the specific ecology for such analyses.
- To account for discontinuous distributions, numerical and range-border related indices of marginality might be more suitable than categorical definitions or centre-based indices for studies of centre – periphery gradients.

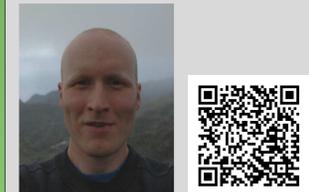
References

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partially funded by



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