

The expectations of the island theory revisited by molecules in the heather *Erica scoparia* s.l.: an answer to the Azorean enigma

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We revisited the Azorean enigma based on the fact that Azorean endemic species tend to be more widespread than Canarian ones despite the larger distances among Azorean islands, by revisiting the expectations of the island theory on the patterns of genetic diversity and structure in the heather *Erica scoparia* s.l.

For this purpose we aim to address the following questions :

- Do island populations exhibit reduced levels of genetic diversity as a result of founding effects? What are the distribution patterns of genetic variation?
- To what extent are populations connected by pollen and seed-mediated gene flow, and at which scale does isolation by distance operate?
- As a consequence, what are the contributions of in-situ diversification, either resulting from isolation by distance among islands or sympatric radiation, and recruitment from continental areas, in the present patterns of genetic diversity?

- *E. scoparia* s.l. is a taxonomic complex comprised of four taxa: *E. scoparia* L. s.str. distributed across the western Mediterranean, extending eastwards to west central Italy, northwards to west-central France, and southwards to the Mediterranean fringe of Morocco and Tunisia ; *E. scoparia* subsp. *azorica* endemic to the Azores ; *E. scoparia* subsp. *maderinicola* endemic to Madeira and *E. scoparia* subsp. *platycodon* endemic from the Canary Islands (Tenerife and La Gomera).

- 109 specimens were sampled from the entire distribution range of *E. scoparia* s.l.

- Each specimen was genotyped at the cpDNA loci *matK* and *trnH-psbA* and the nDNA at103

- Population genetic techniques (F_{st} , N_{st} , F_{ij} , N_{ij} , genetic diversity calculations and fuFs) were used on cpDNA and nDNA loci as well as genotype network reconstruction and niche modelling techniques (Maxent)

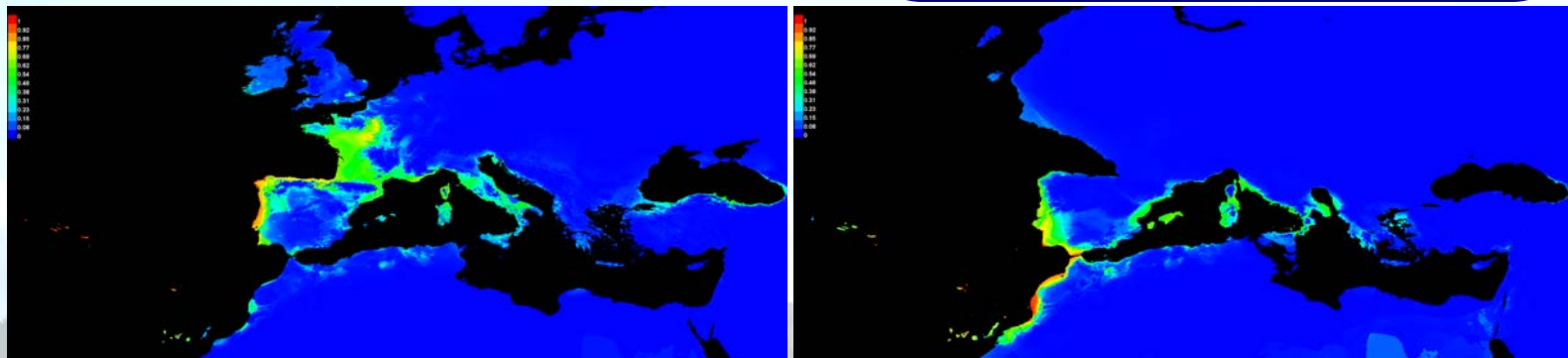


Fig. 1. : Present (left) and LGM (right) potential distribution of *E. scoparia* inferred with Maxent.

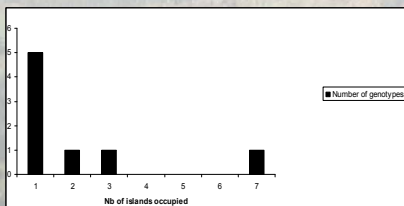


Fig. 3. Mean M_j resulting from the comparisons of the cpDNA haplotype (*matK* and *trnH-psbA*) and nDNA allele at the *at103* locus between pairs of individuals of the heather *Erica scoparia* s.l. in the Azores depending on the geographic distance separating them.

Fig. 2. Frequency distribution of combined cpDNA (*matK* and *trnH-psbA*) and nDNA (*at103*) genotypes in the heather *Erica scoparia* s.l. in the Azores.

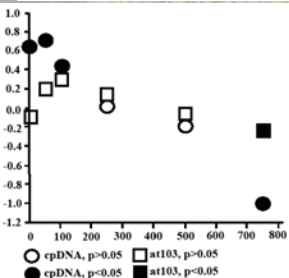


Fig. 4. Genotypic network resulting from the analysis of combined cpDNA *matK* and *trnH-psbA* and nDNA *at103* gene sequences (*at103* heterozygotes excluded) in 82 specimens of the heather *Erica scoparia* s.l. across its entire distribution range.

Results and discussion

The comparison of the extant and reconstructed distribution range 10,000 years ago for *E. scoparia* (Fig.1.) reveals an increase in macroclimatic niche availability. The species is still absent from potentially suitable areas, as western Canary Islands or the UK, wherein pollen records from the Gortian interglacial testify of the presence during the middle Pleistocene (Nelson, 2009). Altogether, this suggests that *E. scoparia* has not (re)colonized all of its potential distribution range, which is in line with an increasing body of evidence for a global signal of expansion in the Mediterranean flora.

- A phylogeographic signal in the cpDNA but not in nDNA points to a globally pollen mediated gene flow among populations from different geographic area (cpDNA: $N_{st}=0.65 > F_{st}=0.39$; $p < 0.05$ / nDNA : $N_{st}=0.78$ non significantly higher than $F_{st}=0.71$)

-The lowest cpDNA pairwise F_{st} value of 0.01 was observed between the Azores and the continent: this suggests that part of the genetic diversity observed in the Azores results from seed recruitments from the continent.

-A curve of genotypic diversity in the Azores (Fig.2.) with its mode on single island endemics suggests that the Azorean Enigma needs to be reformulated: infra-specific diversification does occur in the Azores and single-island endemics are more common than widespread ones, but this diversification is not followed by a morphological one.

-Within the Azores, the steep slope of the regression between pairwise kinship coefficients and geographic distance in the cpDNA (Fig.3.) indicates limited seed-mediated gene flow that is likely to favour allopatric diversification in the Azores.

Conclusions

While those results challenge the taxonomic identity of *E. azorica* as an Azorean endemic species since the network of genotype relationships indicates that it is comprised of two groups of haplotypes corresponding to at least two colonization events, they highlight the biogeographic significance of the Azores in the evolutionary history of the species. In particular, the very high genetic diversity in islands, as opposed to the expectations of the island theory, is reminiscent of similar patterns that have recently been interpreted in terms of the role of Macaronesia as a refugium for the European and North African floras during the glaciations (Laenen *et al.*, 2011). Although the direction of gene flow could not be established in the case of *E. scoparia*, the diversification and expansion of the latter, which gave rise to a Madeiran endemic genotype, two Canarian endemics along with the evidence for both seed- and pollen mediated gene flow between the Azores and the continental areas, definitely support the idea, that islands are not the end of the colonization road (Bellemain & Ricklefs, 2008) and might actually play a significant role in the evolution of continental biodiversity.