Genetics of hybrid speciation in *Senecio* (Asteraceae)

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*S. aethnensis*

*S. chrysanthemifolius*

*S. squalidus*
The *Senecio* hybrid zone on Mount Etna, Sicily.
**Senecio squalidus**: introduction and spread in the UK

Cultivated in Oxford Botanic Gardens from 1700 for 150+ years.

Spread along railway lines during industrial revolution from 1800+.

Project objectives

Describe molecular and quantitative differentiation between species

Measure selection and identify its molecular and quantitative genetic targets

Investigate interactions between genetic architecture and species differentiation
Research strategies

Wild-sampled glasshouse-grown population samples and large interspecific $F_2$ families

Multiple quantitative trait measures

Molecular marker development and genotyping

Population genetic analyses of molecular and quantitative differentiation between species

Genetic and quantitative trait locus (QTL) mapping and analyses
Quantitative genetic traits

Twenty quantitative trait measures divided into six groups of related traits

(1) Seed  (2) Leaf  (3) Floral

(4) Architecture  (5) Ecophysiology  (6) Growth rates
Molecular genetic markers

Allozymes (enzyme electrophoretic variants)

Simple sequence repeats (SSRs or microsatellites)

Random amplified polymorphic DNA (RAPDs) and amplified fragment length polymorphisms (AFLPs)

Expressed sequence tag (EST) markers: SSRs, insertion-deletions (indels)
Differentiation tests for loci under selection

*S. aeth.* versus *S. chrys.*

Dom. AFLPs; dFdist  Codom. markers; LOSITAN

0.31 dom. and 0.35 codom simulated mean $F_{st}$ differentiation

2.7% dom. and 30.0% codom. markers >95% signif. divergent
**Input: (per locus)**

- S. aethnensis obs allele counts
- S. chrysanthemifolius obs allele counts

Assume equal contributions

**Simulation: repeated x 1000**

Bottleneck in Oxford: $n_1$ individuals for $t_1$ years

Escape from Oxford: exponential population increase for $t_2$ years

**Simulated allele counts for current S. squalidus, assuming no natural selection**

**FDIST**

**Output**

- Null distributions of $F_{st}$ for S. squalidus vs each parent
- p-values for $F_{st}$
Genetic maps of $F_2$ interspecies crosses

- **$S. aeth.$ map**  
  (AxC $F_2$ cross)

- **$S. chrys.$ map**  
  (CxS $F_2$ cross)

- **$S. squal.$ map**  
  (SxA $F_2$ cross)
Case study: Ray2 chromosome
Case study: *Ray2 chromosome*

*S. aeth. x S.chrys.* chromosome segregation distortion
Case study: Ray2 chromosome

S. aeth. x S. squal. chromosome segregation distortion

[Graph showing Chi2 value vs. Haldane cM distance with codominant and dominant markers indicated.]
Case study: Ray2 chromosome

*S. chrys.* x *S. squal.* chromosome segregation distortion
Case study: Ray2 chromosome

S. aeth. x S. chrys. quantitative trait loci

Graph showing the distribution of quantitative trait loci with Haldane cM distance on the x-axis and Diff test p value on the y-axis. Markers include Petiole +26%r, Capsize +13%r, Rayarea +16%r, Pappus +31%r, Poorpollen +20%d, Codom markers, Dom markers, Diff test p value, and Diff test threshold.
Case study: *Ray2 chromosome*

*S. aeth. x S. squal.* quantitative trait loci

- Fruitlength +22%d
- Floretnumber -13%d
- Pollennumber +13%r
- Capnumber -17%d
- Internode -15%r

```
+-------------------+
| Internode         |
| -15%r             |
+-------------------+
| Floretnumber      |
| -13%d             |
+-------------------+
| Pollennumber      |
| +13%r             |
+-------------------+
| Capnumber         |
| -17%d             |
+-------------------+
| Fruitlength       |
| +22%d             |
+-------------------+
```

Haldane cM distance

- Codom markers
- Dom markers
Case study: *Ray2 chromosome*

*S. chrys.* x *S. squal.* quantitative trait loci

Branch number +11\% d

Floret number -22\% d

Poor pollen -14\% d

- Codom markers
- Dom markers
Preliminary mapping conclusions

Genomic rearrangements exist between these closely related *Senecio* species (marker order, segregation distortion, fertility)

Genetics of species differences relatively simple (few QTLs of intermediate effect per trait and overlapping QTLs for different traits)

No good candidate loci for species differences yet (population differentiation or QTLs but not both)
Acknowledgements

- Colleagues (St Andrews): Richard Abbott, Daniel Barker and Paris Veltsos
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- Technicians: David Forbes and Harry Hodge
- Project students: Ail-Lan Wang, Amy Millar, Cameron Hunt
Quantitative genetic hybrid cline variation

Hybrid index

Distance (km)

- Arch
- Flor
- Leaf
- Seed
- Gen
Indirect estimates of selection and dispersal

<table>
<thead>
<tr>
<th>Marker type/ Parameter estimate</th>
<th>Molecular genetic</th>
<th>Quantitative genetic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cline width (km)</td>
<td>3.24</td>
<td>2.38</td>
</tr>
<tr>
<td>Elevation in disequilibrium\covariance</td>
<td>0.03</td>
<td>0.03</td>
</tr>
<tr>
<td>Recombination rate</td>
<td>0.1 – 0.5</td>
<td>0.1 – 0.5</td>
</tr>
<tr>
<td>Dispersal rate generation\1(km)</td>
<td>0.17 – 0.38</td>
<td>0.24 – 0.54</td>
</tr>
<tr>
<td>Selection against hybrids(%)</td>
<td>2.2 – 11.2</td>
<td>8.1 – 40.6</td>
</tr>
<tr>
<td>Generations of contact</td>
<td>11 – 57</td>
<td>3 – 16</td>
</tr>
</tbody>
</table>

**Molecular and quantitative genetic differentiation**

**Molecular markers (22 SSR, allozyme and indel loci)**

**Quantitative markers (20 traits)**

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**Senecio squalidus** is distinct from Sicilian hybrid *Senecio*, particularly for molecular genetic markers.
## Quantitative genetic differentiation

<table>
<thead>
<tr>
<th>Ranked contribution</th>
<th>1&lt;sup&gt;st&lt;/sup&gt; principal coordinate (S. aeth v. S. chrys)</th>
<th>2&lt;sup&gt;nd&lt;/sup&gt; principal coordinate (S. squal v. Sicilian Senecio)</th>
</tr>
</thead>
<tbody>
<tr>
<td>First</td>
<td>Fruit length</td>
<td>Plant height</td>
</tr>
<tr>
<td>Second</td>
<td>Leaf dissection</td>
<td>Days true leaf to flowering</td>
</tr>
<tr>
<td>Third</td>
<td>Floral display area</td>
<td>Days germination to true leaf</td>
</tr>
<tr>
<td>Fourth</td>
<td>Leaf base width</td>
<td>Photosynthesis at 7 C</td>
</tr>
<tr>
<td>Fifth</td>
<td>Pappus (parachute) length</td>
<td>Branch number</td>
</tr>
<tr>
<td>Sixth</td>
<td>Floret number</td>
<td>Photosynthesis at 20 C</td>
</tr>
</tbody>
</table>
Senecio squalidus is differentiated from Sicilian Senecio for both molecular markers and quantitative traits (Fst and Qst).
**Molecular genetic differentiation**

- **Senecio squalidus** has fewer alleles in common with parental species than Sicilian hybrids.
- Allele frequency differences are greater for paired comparisons involving *S. squalidus* than Sicilian *Senecio*.
Conclusions: Divergence across a natural hybrid zone

• The *Senecio* hybrid zone is maintained by moderate to strong selection against hybrids despite considerable dispersal

• Quantitative traits for floral, leaf and fruit structures show the strongest signals of divergent selection
Conclusions: Divergence associated with invasiveness

- The population bottleneck associated with the introduction of *S. squalidus* has resulted in considerable molecular genetic divergence from its parental species.

- A different set of quantitative traits differentiate *S. squalidus* and its parents than differentiate the species on Mt Etna.
In progress: Differentiation tests of more loci; Bayescan
*S. aeth.* versus *S. chrys.*

AFLPs  
Codominant markers
In progress: Genetic and QTL mapping of these markers

S. aeth. markers; *aeth x chrys* F2 family; ray area
In progress: Genetic and QTL mapping of these markers

*S. aeth.* markers; *aeth x squal* F2 family; ray area