Population differentiation, local adaptation and gene flow in the fragmented alpine landscape:

Case stories of alpine species

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Alpine habitats

- Life conditions change with altitudes
  - temperature decreasing
  - shorter growing season, more snow
  - harsher environmental conditions
  - landscape: patchy, naturally fragmented
  - habitats and populations more isolated

- How is plant life affected
  - genetic diversity might decrease
  - selection regimes might change
  - differentiation in phenotypic traits are expected

- Adaptations vs. gene flow and random drift
General questions

• Does genetic diversity decrease with altitude? Thereby, does the potential for evolutionary change remain intact?

• How important is population differentiation in important life history traits in alpine plants?

• Is selection pressure strong enough for pronounced adaptation along gradients?

• How important are anthropogenic factors?
I. Genetic diversity

Available studies using molecular markers give little indication for a general decrease of genetic diversity in plants with altitude.

This is particularly true for clonal plants, a frequent life form at high altitudes.
Alpine habitats and genetics

Genetic diversity: hypotheses

• **Within populations**
  – higher in early successional, depleted in marginal habitats

• **Among populations**
  – high genetic differentiation
  – restricted gene flow
  – Isolation by distance pronounced

• **Genetic diversity depends on many factors**
  – life history traits (longevity, reproduction, ...)
  – Breeding system
  – dispersal capacity (wind, animal, ...)
  – glacial history, time since colonization

• **Predictions difficult**
The species

**Epilobium fleischeri**
- Clonal, mixed breeding
- 1000 - 2700 m a.s.l.
- Glacier forelands, river beds
- Swiss web flora (www.wsl.ch)

**Geum reptans**
- Clonal, outbreeder
- 1950 - 3200 m a.s.l.
- Glacier forelands, screes

**Campanula thyrsoides**
- Monocarpic outbreeder
- 1300 - 2800 m a.s.l.
- Grasslands, screes
Particular Questions

**General:** How large are effects of landscape fragmentation on molecular diversity within and among population of alpine plant species?

- We expected population differentiation to be high and to increase with distance due to natural fragmentation and patchyness.
- We expected lower genetic differentiation for the species with pronounced adaptation to seed dispersal (*Epilobium*).
- We expected differentiation to be larger in the short-lived, monocarpic *Campanula* compared to the long-lived clonal species *Geum* and *Epilobium*. 
Methods

Sampling
- Sites spread over the Swiss Alps
- 20 (32) Populations, 20 Individuals
- Similar altitudinal range: 1000 m
- Similar geographic range: 200 (-330) km
- Extended sampling in Campanula

Marker
- RAPD

Dispersal measures
- Pollen flow (direct observation)
- Seed production (measurement)
- Seed dispersal (explicit modelling)

Data treatment
- Standardization
- Repeated calculations with varying F_{is}
Location of populations

Epilobium fleischeri  Geum reptans  Campanula thyrsoides

Dashed line is approximate border line between 2 glacial refugia (Schönwetter et al. 2005)
Dispersal

Epilobium fleischeri >> Geum reptans > Campanula thyrsoides

4.5 Mio seeds/pop
- 91 % < 10 m
- 8.5 % > 100 m
- 0.5 % > 1 000 m
- 22 000 seeds > 1 000 m

max pollen flow
- 30 m

>10 Mio seeds/pop
- 99.9 % < 10 m
- 0.015 % > 100 m
- 0.005 % > 1 000 m
- 520 seeds > 1 000 m

max pollen flow
- 30 m

1.5 Mio seeds/pop
- 99.9 % < 10 m
- 0.001 % > 100 m
- 0.001 % > 1 000 m
- 15 seeds > 1 000 m

max pollen flow
- 39 m
Genetic diversity and altitude

- No effect of molecular diversity with population size
- Molecular diversity related to altitude only in *Epilobium*
- No differences between early and late succession in *Geum*

\[
H_e = 0.19 \\
H_e = 0.21 \\
H_e = 0.20
\]
Population differentiation

$\Phi_{st} = 22.7\%$

$\Phi_{st} = 14.8\%$

$\Phi_{st} = 16.8\% (27.2)$

Epilobium fleischeri

Geum reptans

Campanula thyrsoides

$pops = 20$

$loci = 47$

$pops = 20$

$loci = 47$

$pops = 32$

$loci = 47$

Stable branches between population pairs separated < 2 km

Populations in close vicinity do not consistently group together
Isolation by distance

- Genetic differentiation increases with distance
- Gene flow likely among more close populations
Glacial refugia for alpine plants

Schönswetter et al. 2005

Campanula thyrsoides

strong molecular differentiation between 2 group of populations from proposed areas of postclacial migration

Campanula thyrsoides
AMOVA:
Variation among regions = 5.39 %
p > 0.001

Microsatellite study with C.t.

Structure = divides the sampled individuals into a number of clusters (K) based on multilocus genotypic data.
Summary: Microsatellites *Campanula thyrsoides*

- High within-population diversity ($H_E = 0.76$)
- Relatively low inbreeding coefficient ($F_{IS} = 0.022$)
- Altitudinal location and size of populations = no effect on molecular diversity
- Moderate genetic differentiation ($F_{ST} = 0.103$)
- Significant isolation-by-distance relationship
- Significant geographic substructure coinciding with proposed postglacial migration patterns
Summary: molecular studies

- **Genetic diversity within populations**
  - similar in all three species
  - not strongly related to altitude
  - high even in small populations

- **Genetic differentiation among populations**
  - relatively moderate
  - isolation by distance (alpine patchyness)
  - not directly related to dispersal capability
  - not particularly strong in the short-lived monocarpic species
  - strong stochastic component at all scales (founder effects, bottle-necks)
  - related to glacial history *(Campanula)*
Genetic diversity in *Poa alpina*

The most important fodder grass in the montane and alpine belt of the Alps

A microsatellite study with 74 populations from 12 villages and 24 natural and 50 agricultural used sites

Genetic diversity:
- Increasing with altitude
- Genetic differentiation increasing with distance
- Higher in grazed compared to mown sites

The increase of genetic diversity with altitude may result from an increase of vegetatively reproducing “ecotypes”, thereby increasing overall diversity
What we can learn from the case studies?

• No severe consequences of the naturally fragmented alpine habitats for genetic diversity

• Population are less differentiated than expected

• Gene flow is probably larger than observed by direct observation of pollen and seed dispersal

• But: not high enough to mask imprints of glacial history

• Population differentiation due to landscape structure (isolation by distance) is usually present

• Human impact on genetic diversity (*Poa alpina*)
II. Population differentiation

Phenotypic trait differentiation among populations is probably more the rule than an exception. However, it is less clear:

- how much such differentiation is shaped by altitude, by other factors, or by random drift
- to what extend differentiation is adaptive
- to what extend differentiation in one traits is correlated with other traits (i.e. in the case of seed size)
Sex and Clones in *Geum reptans*

**Sex:** flower heads ≈ 90 wind-dispersed seeds

**Clones:** aboveground stolons with daughter rosettes

*Sexual reproduction*  
*Clonal reproduction*
Complex life cycle of *Geum reptans*
Stochastic population model

How much do sexual and clonal reproduction contribute to population growth?

\( \lambda = 1.067 \) (full model)
\( \lambda = 1.058 \) (25% reduction of sex), \( \lambda = 1.059 \) (25% reduction of clonal growth)
\( \lambda = 1.051 \) (50% reduction of sex), \( \lambda = 1.051 \) (50% reduction of clonal growth)
\( \lambda = 0.974 \) (100% reduction of sex and clonal growth)

Weppler, Stoll & Stöcklin 2006
Clonal growth in *Geum reptans*

The importance of clonal growth tends to increase with altitude!


**Question?**

Does the relative importance of clonal reproduction increase with altitude and successional age? A study with 20 populations of *Geum reptans* from low and high altitude, and from early and late succession.

**Variation in the frequency of stolons:**
- due to size class (p<0.05)
- among populations (p<0.05)
- but not related to altitude or succession (n.s.)
- **But:** Plants from marginal habitats (low and high altitude) invested more in stolons

**Conclusion:** Individual variation and local environmental conditions are more important than environmental gradients!

Weppler & Stöcklin 2005
Adaptation in *Geum reptans*

**Adaptation?**

Experiments in the greenhouse with populations of different origin

Questions:

- Does reproductive behavior change in contrasting habitats?
- Are there interactions between origin of populations and environmental effects (competition, temperature)?

Plants from early successional habitats tended to produce more flowers in the competition free treatment, whereas plants from late successional habitats produced more with competition.

**Conclusion:** Plants from late successional habitats are better adapted to competition.

Limited adaptation, but high size dependent plasticity!

Pluess & Stoecklin 2005
Adaptation in *Poa alpina*

Adaptation to altitude!

- At high altitude: more vegetatively reproducing plants
- At low altitude: more seed producing plants
- Reproductive biomass decreasing with altitude

Adaptation to land use!

- Grazed sites: Allocation to reproduction is higher, indicating advantage of high establishment rates
- Mown sites: more vegetative biomass, favoring competitive strength

Weyand et al., submitted
Seed weight and altitude

A long lasting debatte: does seed size increase with altitude?
Baker 1972 vs. Landolt 1976

Hypotheses: Larger seeds should have a better chance in habitats with harsh environmental conditions. Between and within species a similar trend for increasing seed weight should be observed.

Results:
• Between 29 related species pairs from low and high altitude: Seeds of alpine species with 28 ± 8% heavier seeds.

Conclusion: Selection for species with heavier seeds at higher altitude.

• However: within species no such trend was detected
  The trend does not operate across all cases (in 16 of 29 species pairs)
  Co-variation among traits may constrain the correlation between altitude and seed weight, high gene flow may homogenize populations

Conclusion: Constraints may operate against selection the closer populations and species are related to each other

Pluess, Schütz & Stöcklin 2005
Conclusion: Adaptation

The potential for **evolutionary responses** to environmental change is likely to be largely intact.

- Population and trait **differentiation** with altitude is common.
- **Selection** is probably not always strong enough for pronounced changes along gradients.
- **Other factors** like land use or local conditions may override altitude.
- Phenotypic **plasticity** seems to be important for alpine plants.
Glacial history and differentiation?
Acknowledgements

Hafdis H. Ægisdottir
Patrick Kuss
Katrin Rudmann-Maurer
Andrea R. Pluess
Tina Weppler

Markus Fischer (Potsdam)
Felix Gugerli (WSL)
Oliver Tackenberg (Regensburg)
Renata Viti (Basel)

many student helpers

Swiss National Science Foundation