The role of seed provenance in ecological restoration

Armin Bischoff

The role of seed provenance in ecological restoration

1. Why restoration by sowing: dispersal limitation

2. Concepts of restoration by sowing

- Hand collection and hay transfer: why not always possible
- Examples of alternative restoration techniques

3. Problems of restoration by sowing: the provenance question

- Superiority of local origins: theory of local adaptation
- Invasion of superior invasive genotypes
- Ecosystem effects: organisms in other trophic levels
- Outbreeding depression

4. Problems of restoration by sowing: genetic diversity

- Genetic bottlenecks and inbreeding depressing
- Population mixing: outbreeding versus inbreeding depression

5. Conclusions and solutions

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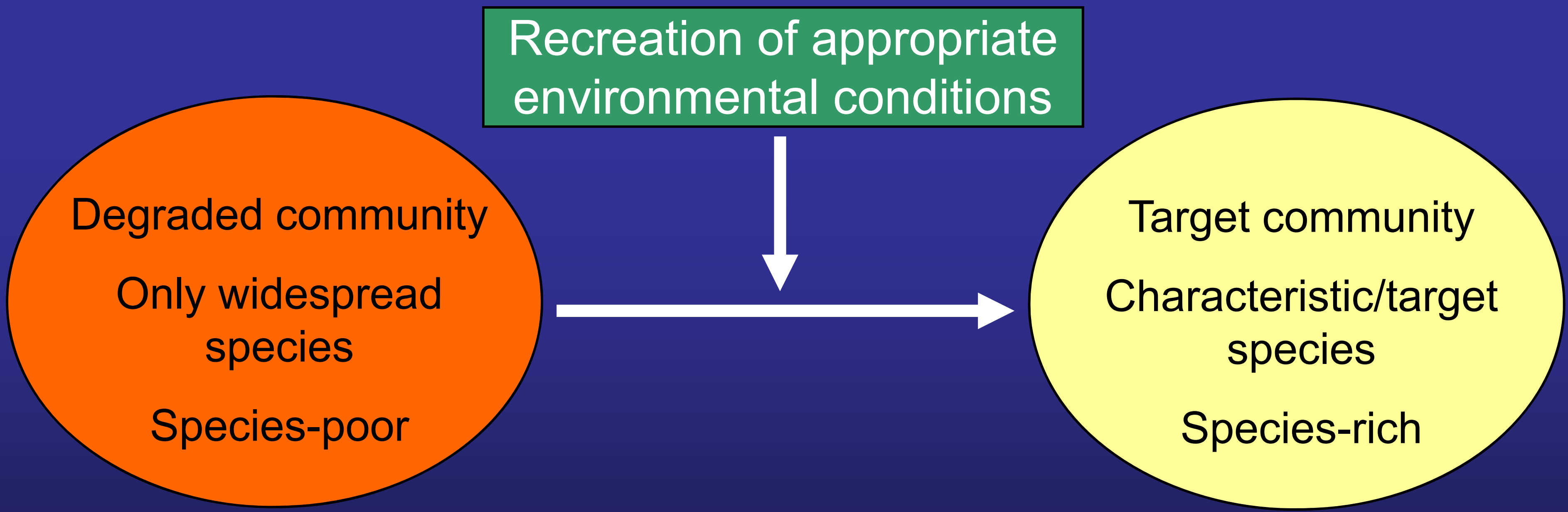
1. Why restoration by sowing

Climax concept of plant succession predicts: same environmental conditions – same species composition and diversity



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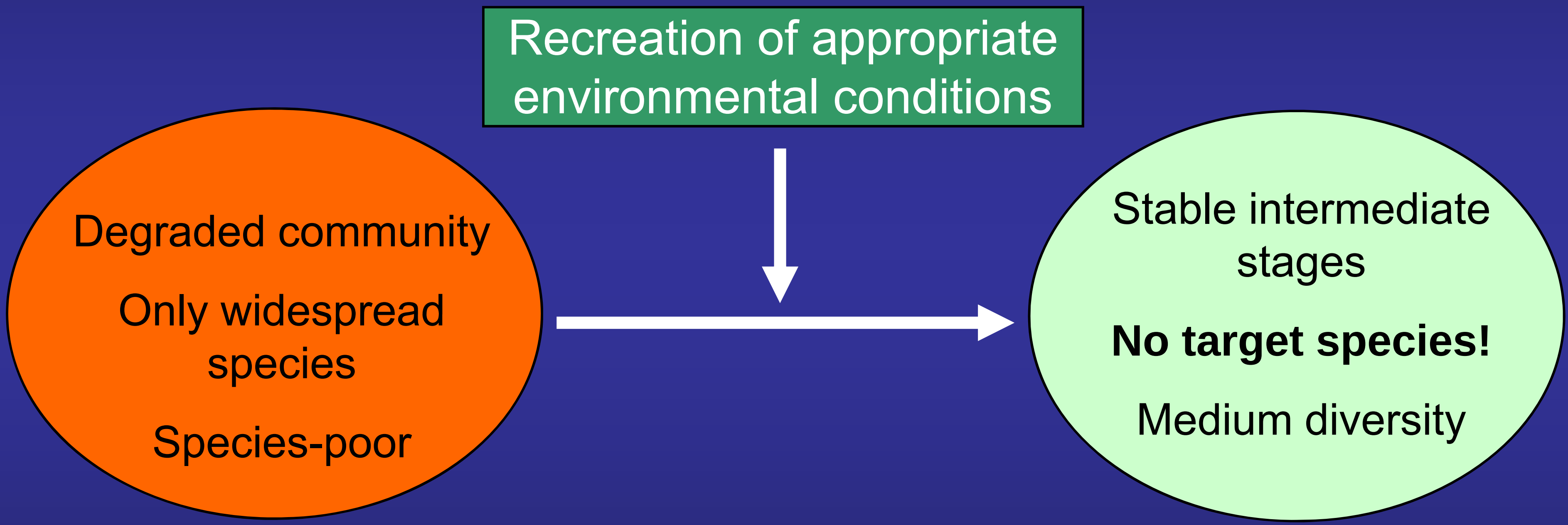
b1 bischofa; 13.09.2008

1. Why restoration by sowing: dispersal limitation

Dispersal limitation: source populations of target species too far away in relation their dispersal capacity



Increase in biodiversity only due to a colonisation by widespread species

1. Why restoration by sowing: dispersal limitation

Example: floodplain grassland restoration (Saale)

- Intensively managed areas: typical floodplain grassland species have disappeared

- 10 years after start of restoration: almost no re-colonisation

1. Why restoration by sowing: dispersal limitation

Example: floodplain grassland restoration (Saale)

- Target community occurs adjacent to restoration sites
- Typical species : *Silaum silaus, Serratula tinctoria, Sanguisorba officinalis, Cnidum dubium, Allium angulosum*

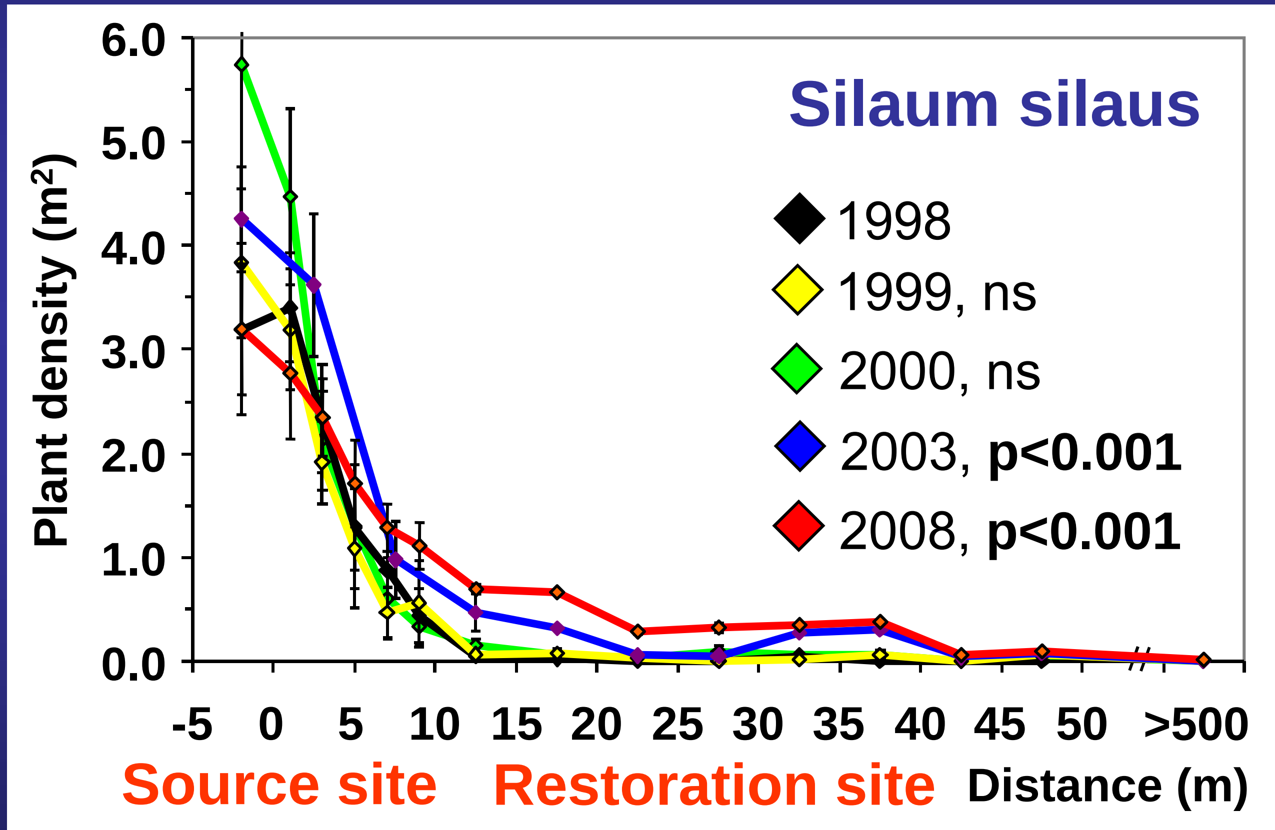
1. Why restoration by sowing: dispersal limitation

Areas in the Saale river valley where species-rich source sites are adjacent to restoration sites provide the possibility to analyse recolonisation in detail

5 transects from source to restoration sites

Density of two target species recorded for 10 years

Small changes in the following years



Considerable increase after 15 years, but density still low and gradient highly significant

Bischoff et al. 2009, J. Appl. Ecol.

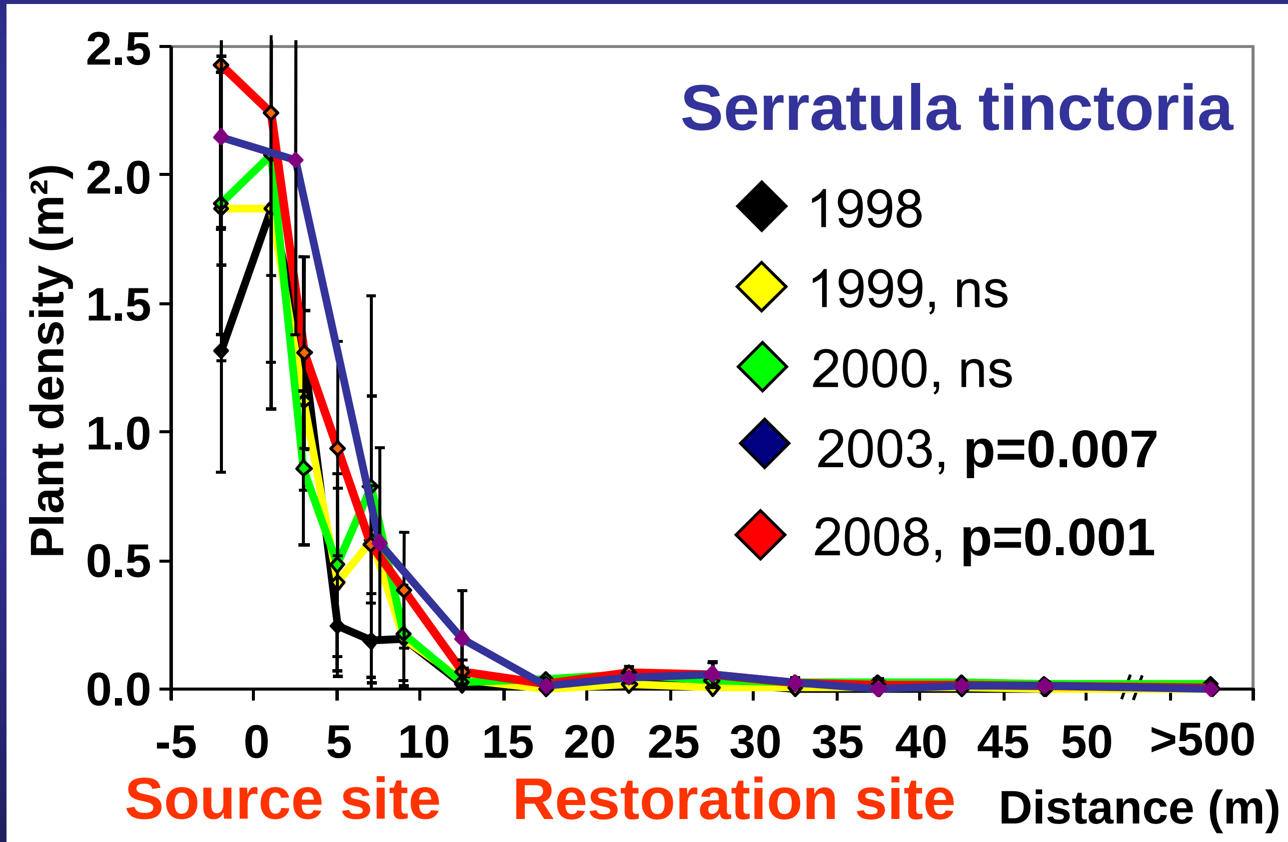
1. Why restoration by sowing: dispersal limitation

Areas in the Saale river valley where species-rich source sites are adjacent to restoration sites provide the possibility to analyse re-colonisation in detail

5 transects from source to restoration sites

Density of two target species recorded for 10 years

Low density of *Serratula* at the restoration site, gradient still significant



Very small changes in the following years!

Bischoff et al. 2009, J. Appl. Ecol.

1. Why restoration by sowing: dispersal limitation

Study at 33 restoration sites (floodplains of Elbe + Saale)

Analysis of factors determining the re-colonisation of target species

Set of 24 explanatory variables including distance to remnant populations of target species

Multiple regression (stepwise forward)

	F_{Step1}	F_{Step2}	Slope (β)
Distance[1]	14.17***	14.17***	-0.566***
$K_{20\text{-}35cm}$	0.56	1.57	-
Elevation	5.54*	1.49	-
$P_{20\text{-}35cm}$	1.53	1.48	-
$pH(KCL)_{0\text{-}20cm}$	0.29	0.88	-
$N_{mineral,\ 0\text{-}20cm}$	1.94	0.85	-
Frequency	0.50	0.72	-
$N_{total,20\text{-}35cm}$	0.39	0.44	-
$C_{total,0\text{-}20cm}$	0.06	0.01	-
Grazed[2]	0.01	<0.01	-

Independent of the order in which variables are fitted distance to source populations the only significant one: confirming the importance of propagule availability and dispersal

[1] >50 individuals, [2] only grazed vs. mown

2. Concepts of restoration by sowing: direct transfer

If colonisation is dispersal limited seed transfer might be a solution

Direct transfer techniques: without propagation in stock

Example hay transfer (Elbe valley, 8 km west of Dessau)

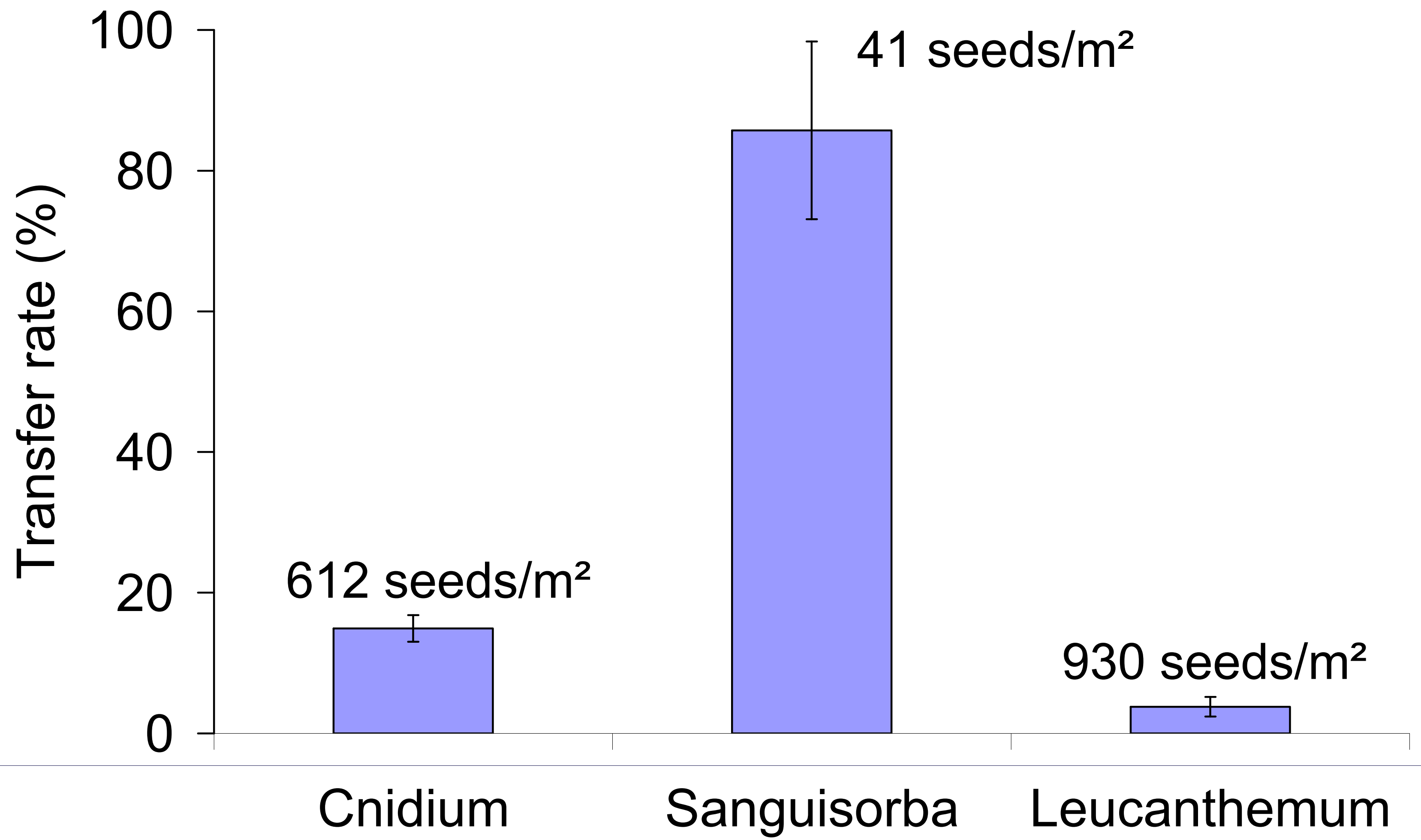
Mowing of an adjacent species-rich site

Transfer of hay to the target site

2. Concepts of restoration by sowing: direct transfer

Quite successful if seeds are ripe at transfer date, multiple transfers would be required to establish all target species

Species-specific differences in transfer rates of ripe seeds



Warthemann, Winter & Bischoff in press, Naturschutz in Sachsen-Anhalt

2. Concepts of restoration by sowing
Direct transfer versus propagation in stock

- Hay transfer very promising if one or two transfers are sufficient, if appropriate source sites of sufficient size are available at a reasonable distance (often not the case) and if restoration sites are not too large
- Hay transfer not possible for all types of habitats (woody plant communities, quarries, wetlands etc.)
- Hand collection only feasible for species re-introduction approaches (small surface, high conservation value)
- Restoration of larger areas usually requires propagation in stock, but – questions of seed provenance and diversity usually more problematic

2. Restoration by sowing: propagation in stock

Propagation of wildflower seeds quite well developed in Switzerland: concept of „ecological compensation“:

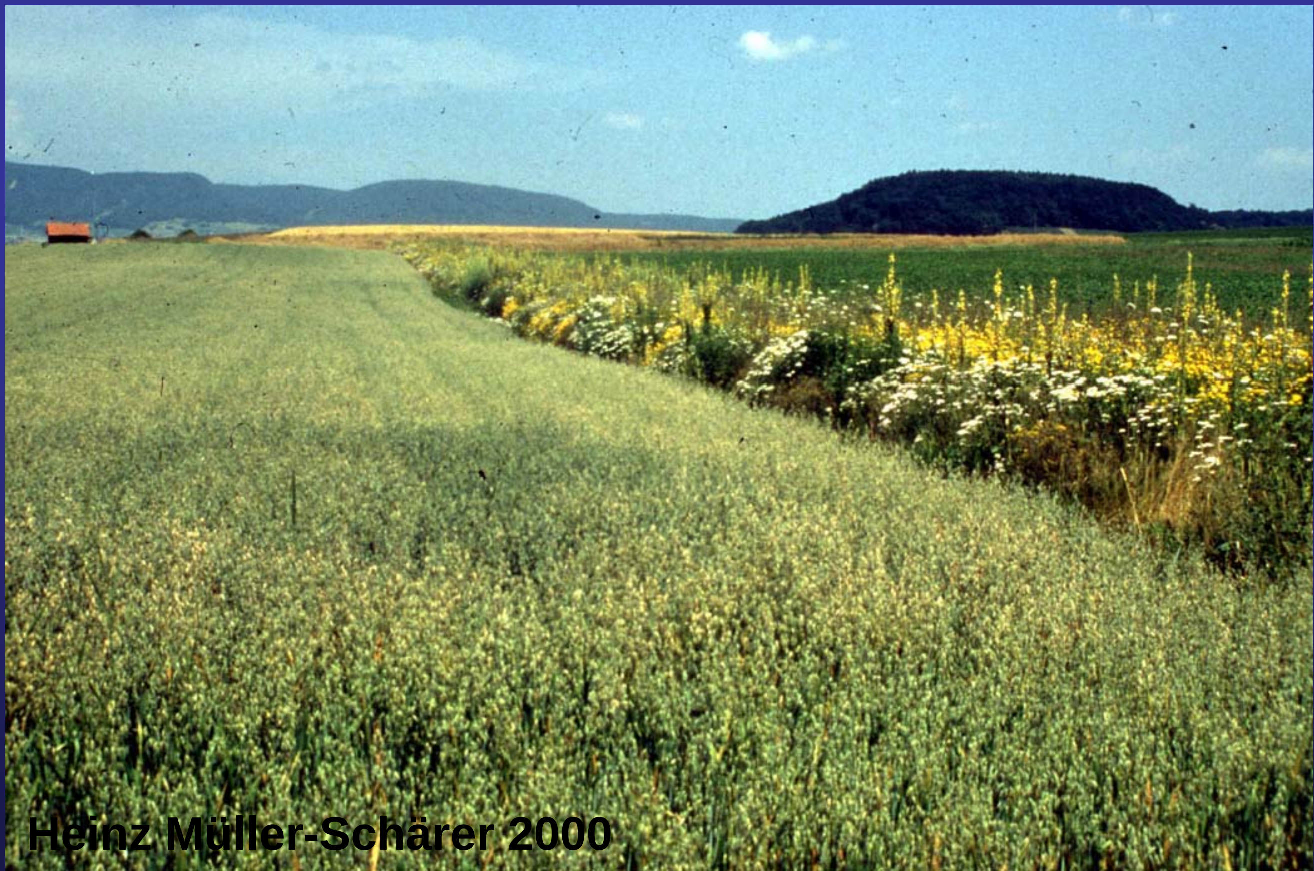
Four grassland mixtures, here „Salvia“ adapted to (medium) dry sites

2. Restoration by sowing: propagation in stock

Most famous example: wildflower strips (Jachères Florales, Buntbrachen, in D known as “Blühstreifen”)

Creation of non-cropped seminatural habitats to restore/ increase plant and associated animal diversity

Mixture of 24 native species, temporal structure (6 years)



Subsidised by Swiss government: 3000-3500 CHF/ha

4% of the farmers
0.2% of total agricultural area (2008)

3. Restoration by sowing: the provenance question

Where and how to collect seed?

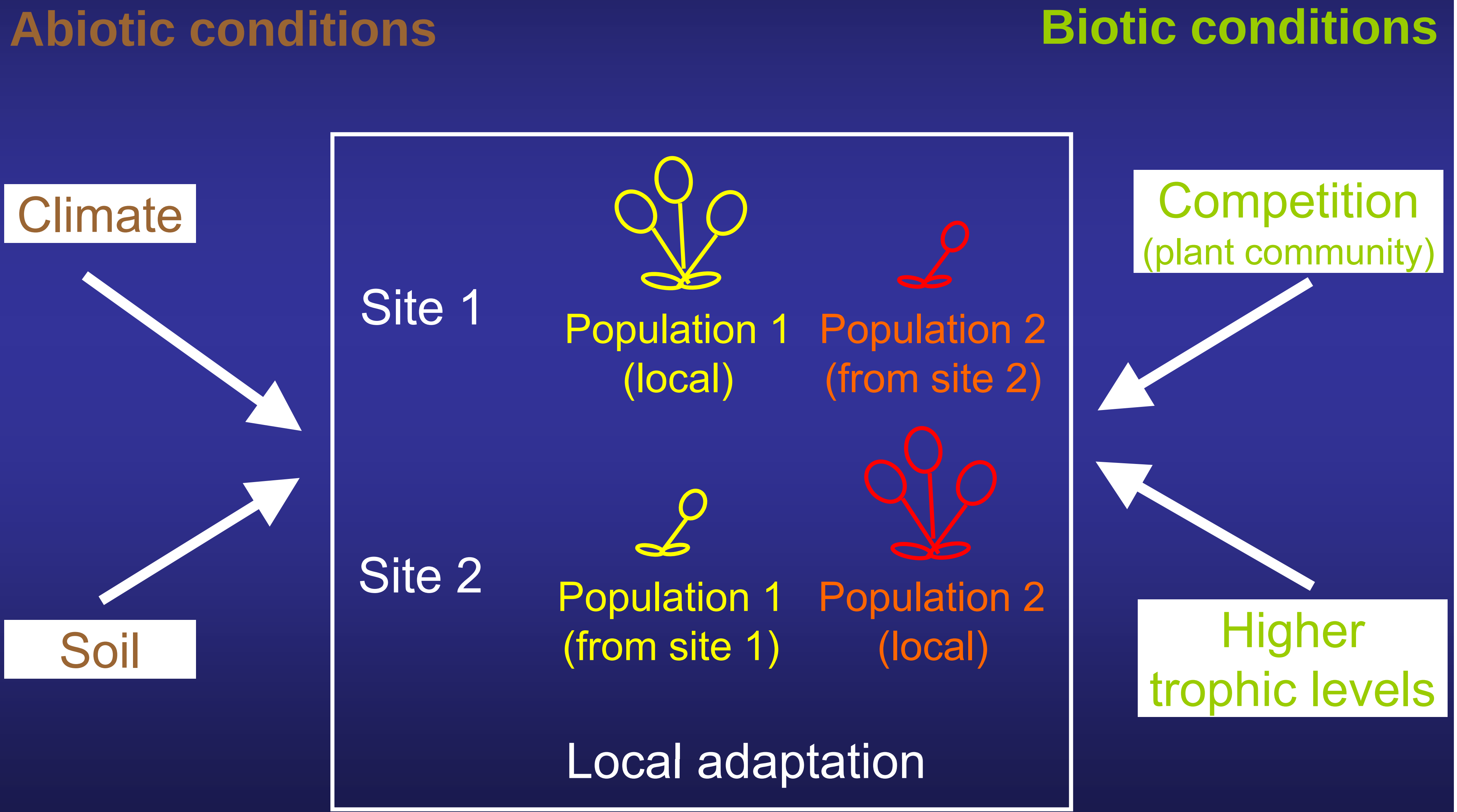
Problem of all approaches if source populations do not occur adjacent to restoration sites

Local material of sufficient genetic diversity is recommended but scales of genetic differentiation are not well known

Possible negative consequences of using non-local provenances

- Poor establishment because genotypes are not adapted to local conditions
- Invasive alien genotypes
- Disturbance of interactions with other trophic levels (ecosystem)
- Outbreeding depression: hybridisations could reduce fitness of still existing local populations

3. The provenance question and local adaptation



3. The provenance question and local adaptation

Test of local adaptation in a reciprocal transplant experiment

Model system: grassland sown on ex-arable land

Species of 3 functional groups:

Non-legume herb : *Plantago lanceolata*

Legume: *Lotus corniculatus*

Grass: *Holcus lanatus*

Second local population from a contrasting habitat to analyse spatial scales of differentiation

3. The provenance question and local adaptation

Block design: 8 replicate blocks

CH	CZ	UK	2nd

No competition,
plots weeded

CH	CZ	UK	2nd

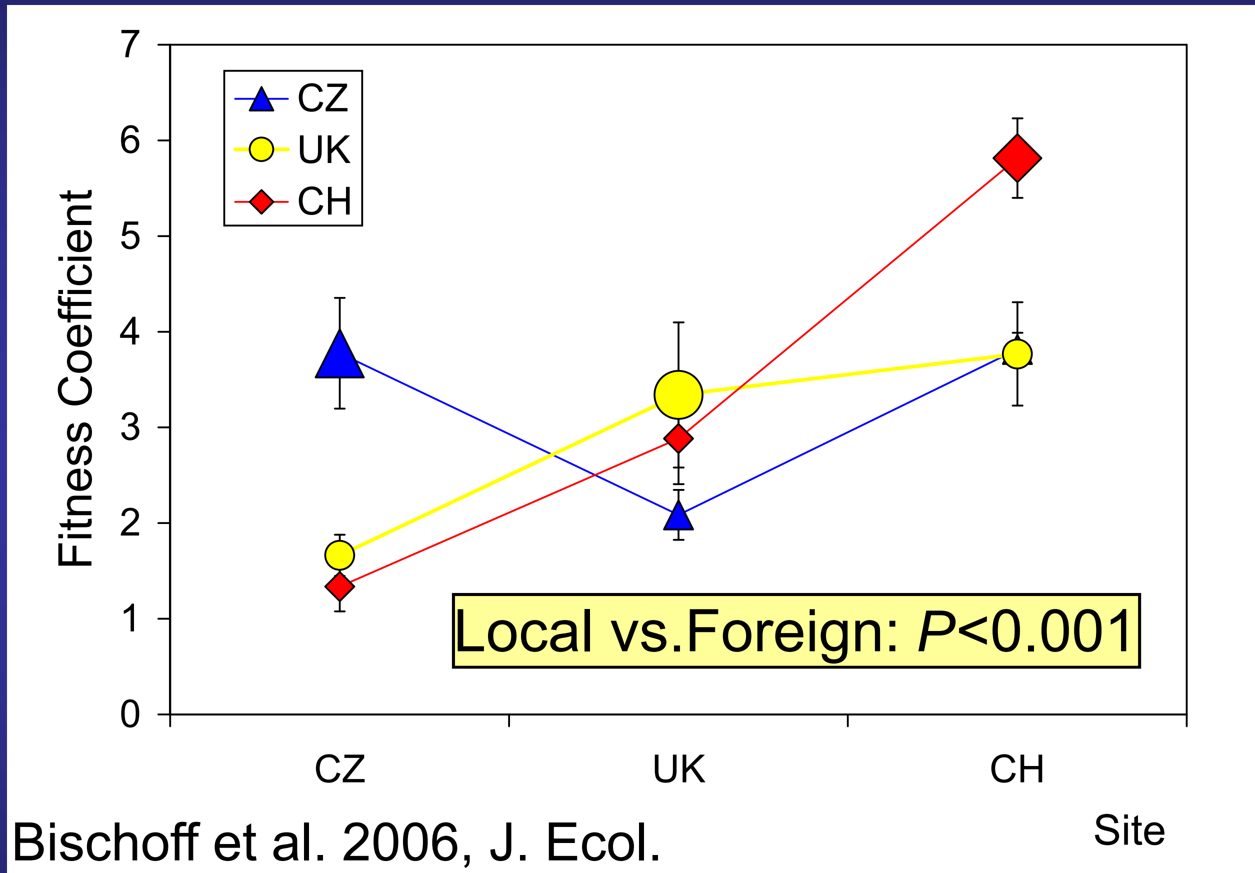
Competition, test species
sown together with resident
grassland community

3. The provenance question and local adaptation

	df	*P*
Site	2	<0.001
Provenance	2	0.037
Prov. x Site	4	<0.001

- Local vs. Foreign contrast

Plantago lanceolata



Fitness coefficient based on germination, survival and reproduction; linear contrast (ANOVA) local vs. foreign significant, local population superior at each site

3. The provenance question and local adaptation

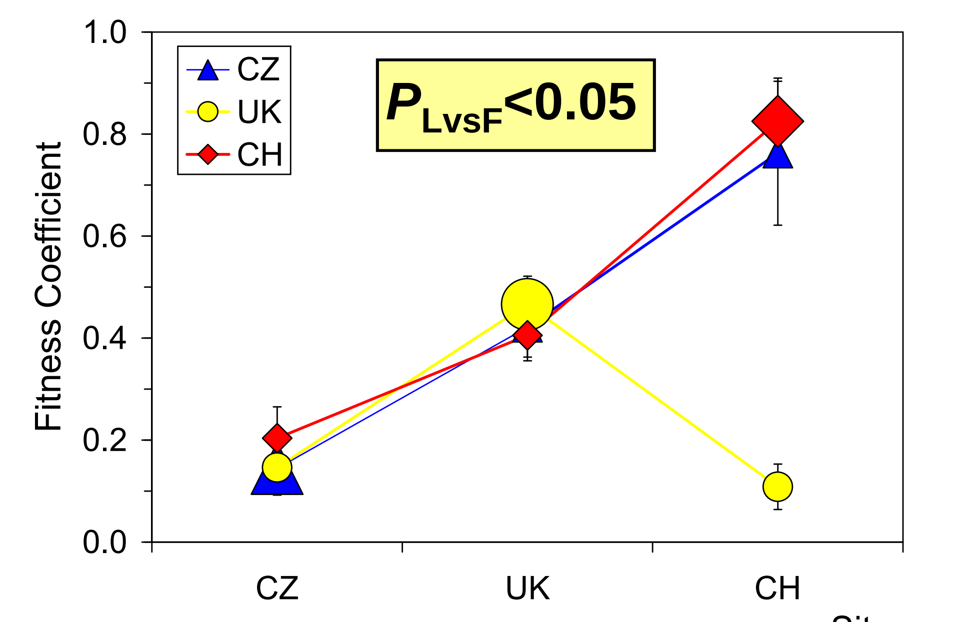
Holcus lanatus: contrast significant but less strong

Local provenance not at each site superior

Lotus corniculatus: No evidence for local adaptation

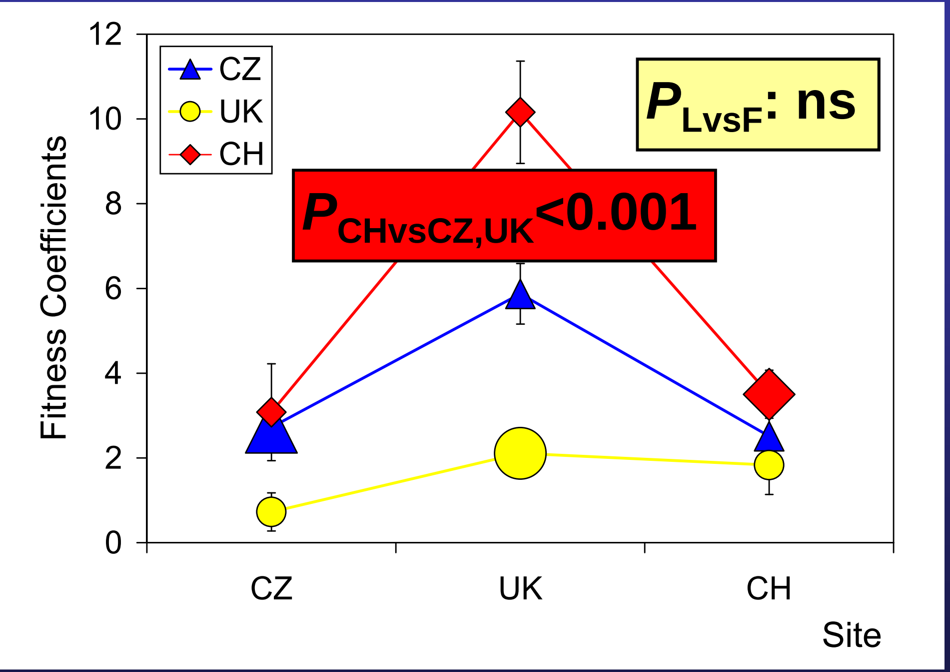
Swiss genotype superior at all sites; effect significant!

Holcus lanatus



Bischoff et al. 2006, J. Ecol.

Lotus corniculatus



3. The provenance question and local adaptation

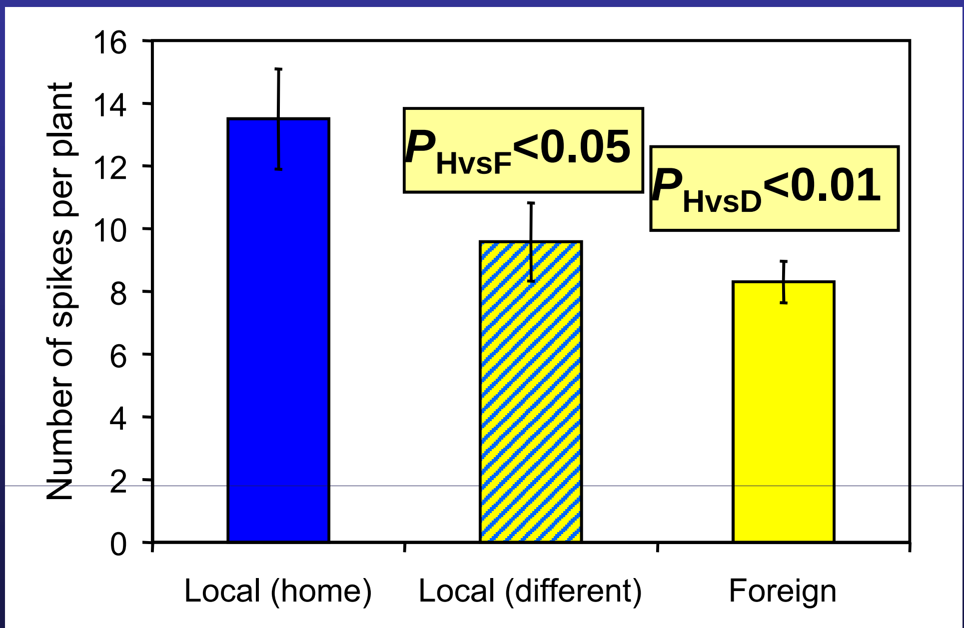
In order to compare differentiation at a local and European scale the following contrasts were calculated:

(1) local “home” (same habitat) versus local “different” (contrasting habitat)

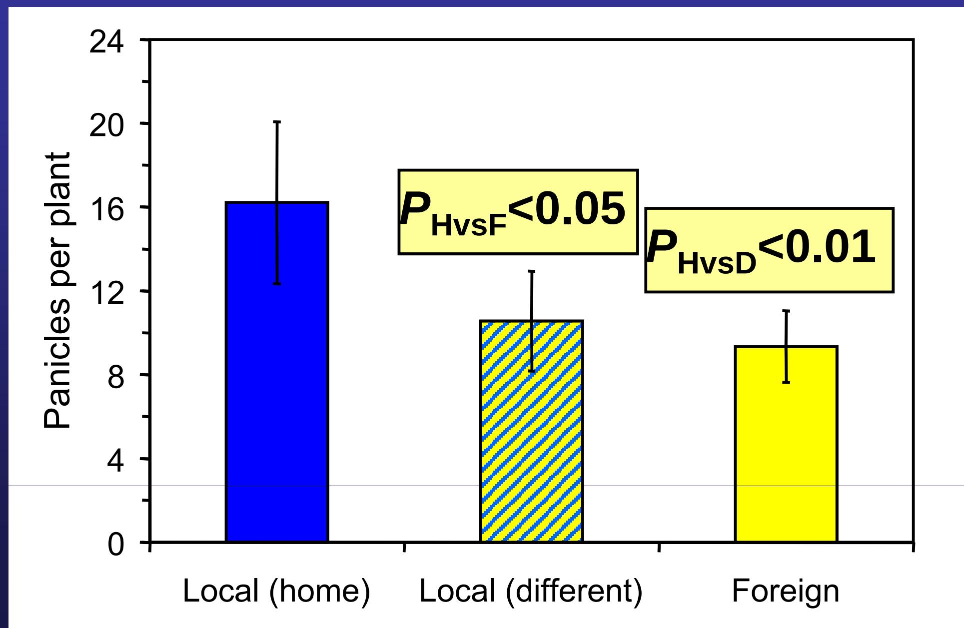
(2) local “home” versus foreign

In nearly all traits with significant local “home” vs. foreign contrasts also local “home” vs. “local” different contrasts significant

P. lanceolata, reproduction

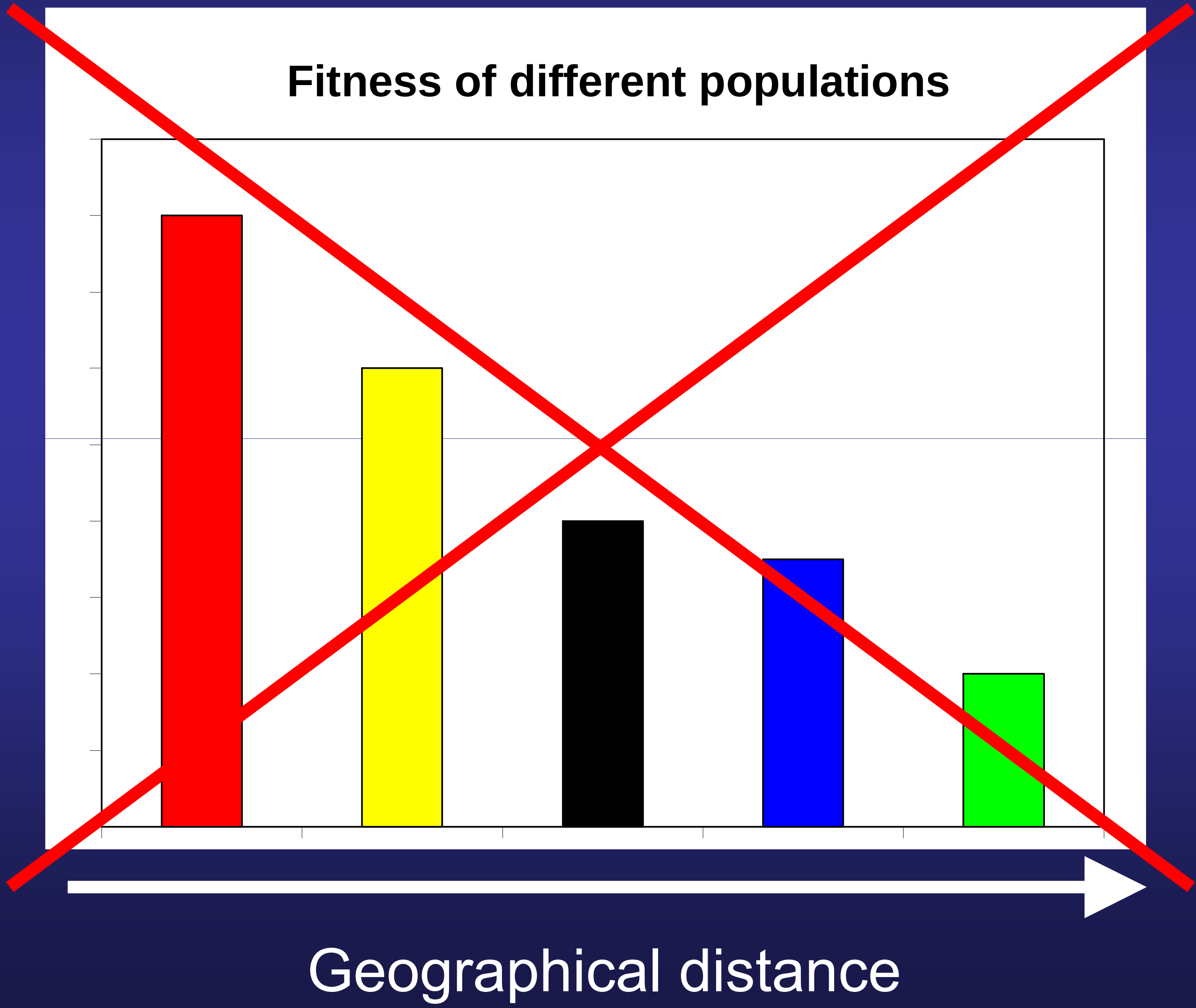


H. lanatus, reproduction



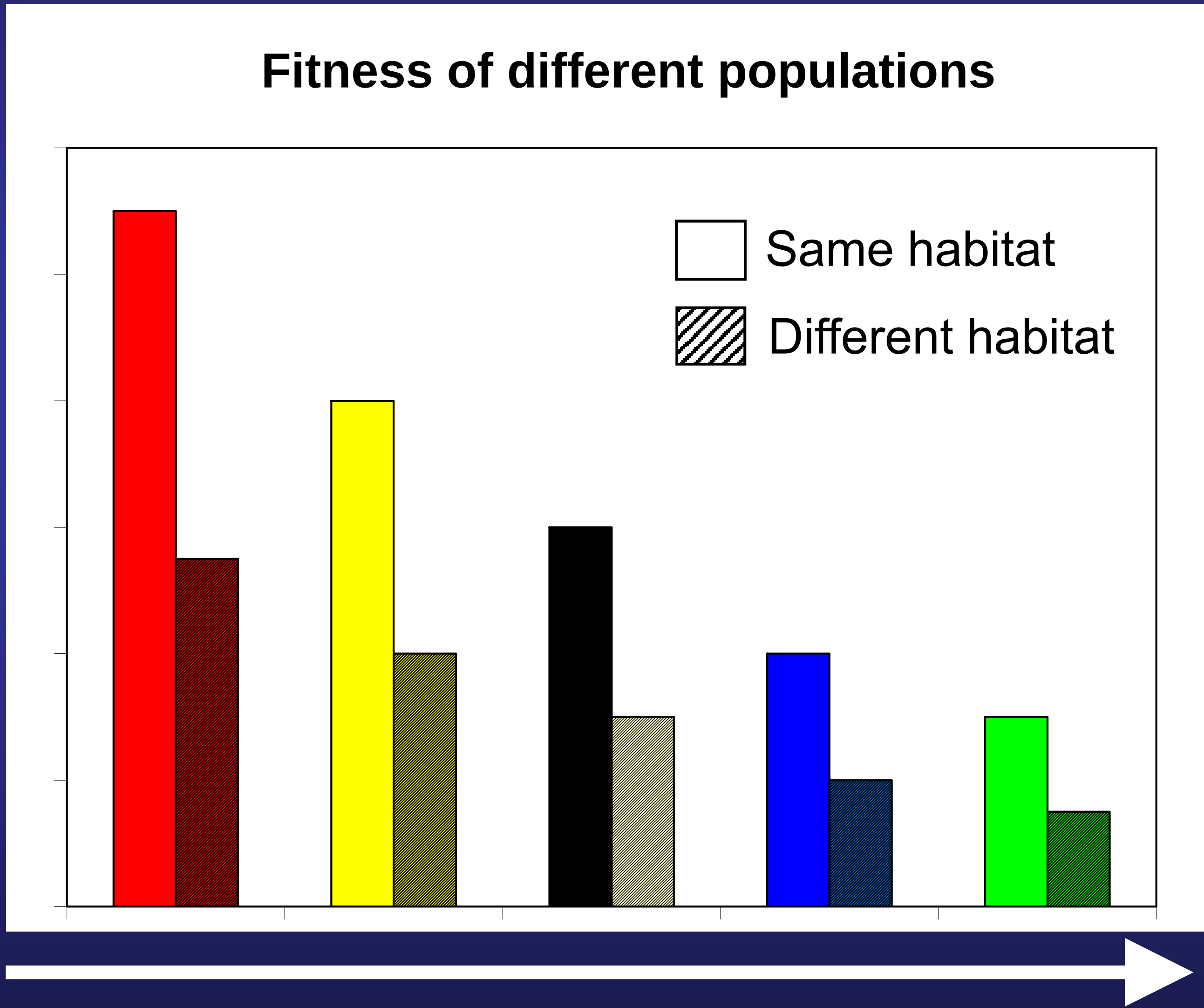
3. The provenance question and local adaptation

No simple relation between fitness and distance of origin because of local habitat differentiation in many species



3. The provenance question and local adaptation

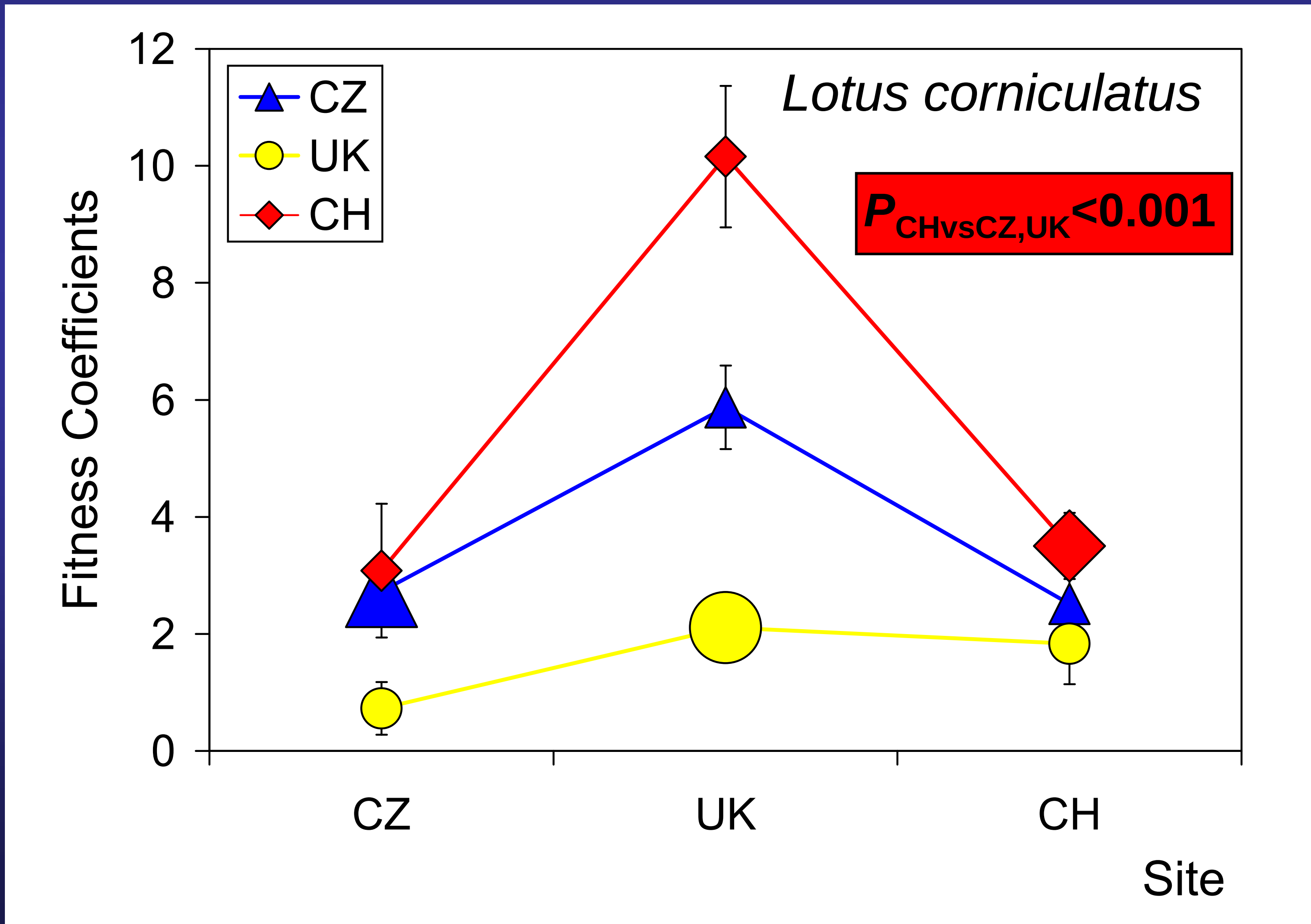
Further research is required to verify whether the model below is more realistic for species occurring in contrasting habitats



Geographical distance

3. The provenance question: invasive genotypes?

There are examples for superior alien genotypes in nearly all studies on local adaptation, even though the local provenance is superior on average: outliers or reality?



3. The provenance question: invasive genotypes?

Cryptic invasion: *Phragmites australis* in North America

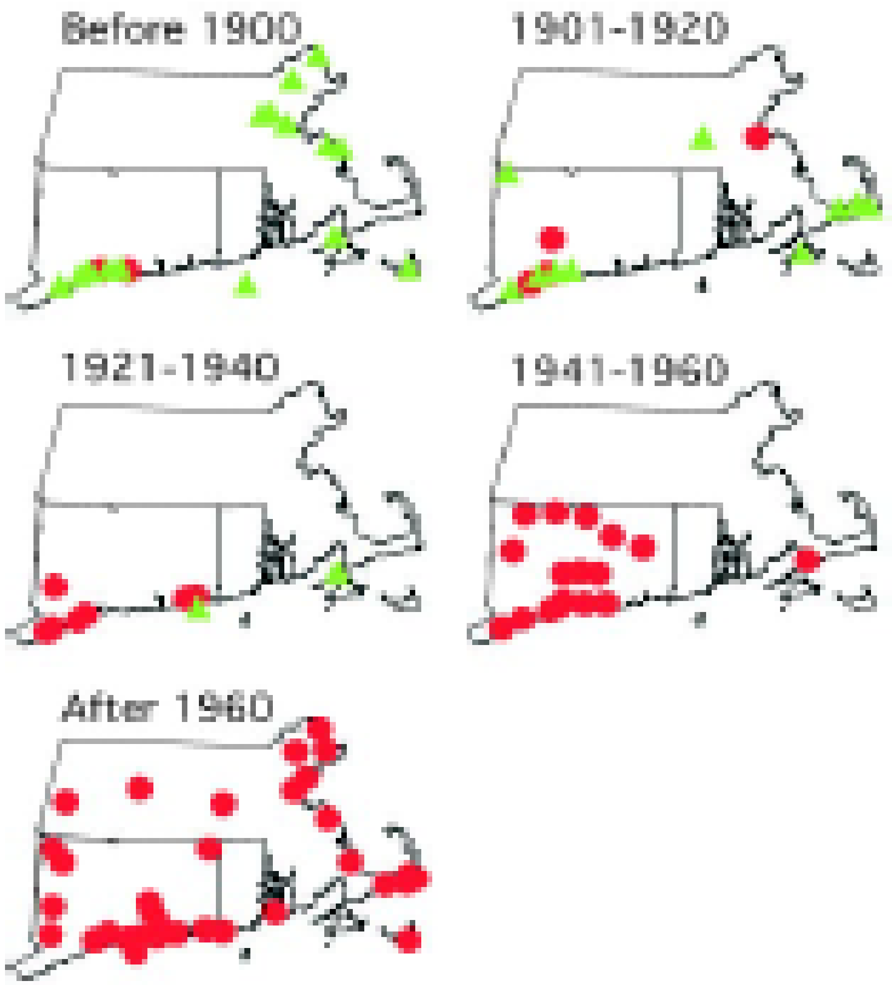


Fig. 2. Changes in *Phragmites* haplotype distribution patterns over 20-year time intervals in Connecticut, Massachusetts, and Rhode Island. Green triangles represent native haplotypes; red circles represent the invasive haplotype M.

Saltonstall (2002) PNAS 99, 2445-2449

Genetic analyses on herbarium plants showed:

Introduced genotype from Eurasia has replaced the native one

The new genotype is more “aggressive”: has expanded to regions previously not known to be occupied by *Phragmites*

Consequences of introducing superior alien genotypes are more serious than a lack of adaptation

3. The provenance question: “ecosystem effects”

Herbivory in *Plantago lanceolata*

Longitarsus leaf beetles (Chrysomelidae), predominantly L. *pratensis* and *melanocephalus*

Specialists on genus Plantago

1. Estimation of damage using categorical scale
2. Sucking samples (Vortex) to analyse beetle no. and diversity

3. The provenance question: “ecosystem effects”

Measurements: Pathogens in *Holcus lanatus*

Puccinia coronata, highly host-specific rust fungus

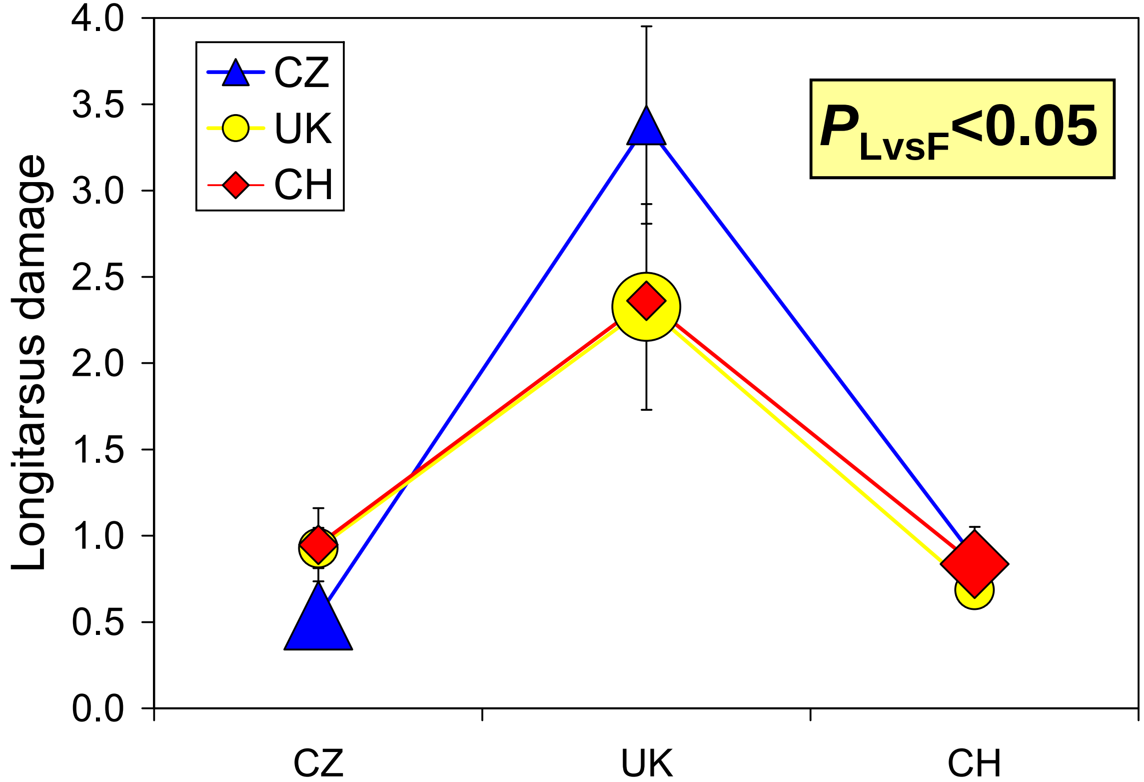
Analysis of infestation in a subsample of 6 leaves per plant using a modified Peterson scale (for crop grasses)

3. The provenance question: “ecosystem effects”

Longitarsus damage on *P. lanceolata*

	df	*P*
Site	2	<0.001
Provenance	2	0.162
Prov. x Site	4	<0.001

- Local vs. Foreign contrast



Cremieux et al. (2008), New Phytologist

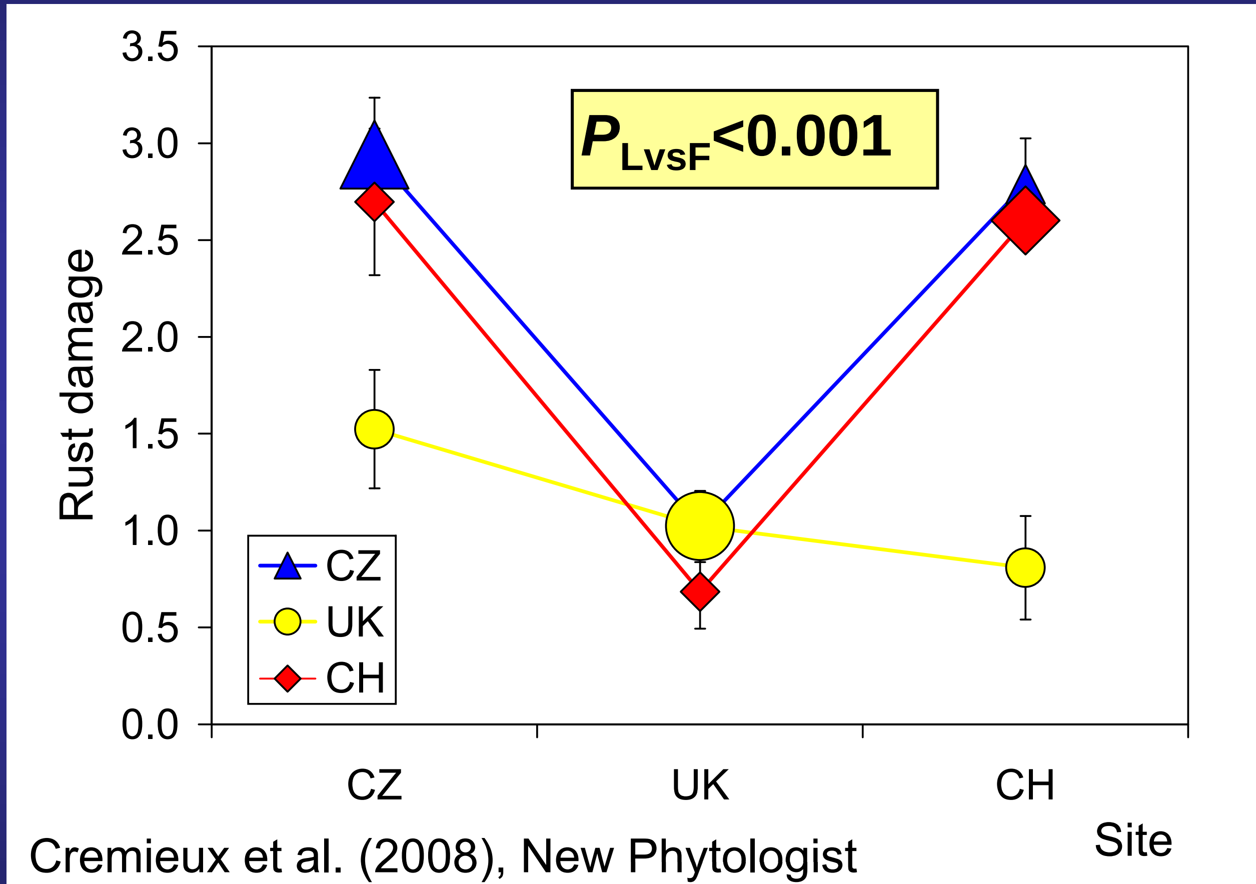
No general provenance effect (main effect not significant) but interaction with site: lower beetle damage on local plants !

3. The provenance question: "ecosystem effects"

Puccinia damage on *Holcus lanatus*

	df	*P*
Site	2	<0.001
Provenance	2	<0.001
Prov. x Site	4	<0.001

➢Local vs. Foreign contrast



Strong overall provenance effect (UK plants less susceptible) and also interaction with site: higher damage on local plants !

3. The provenance question: outbreeding depression

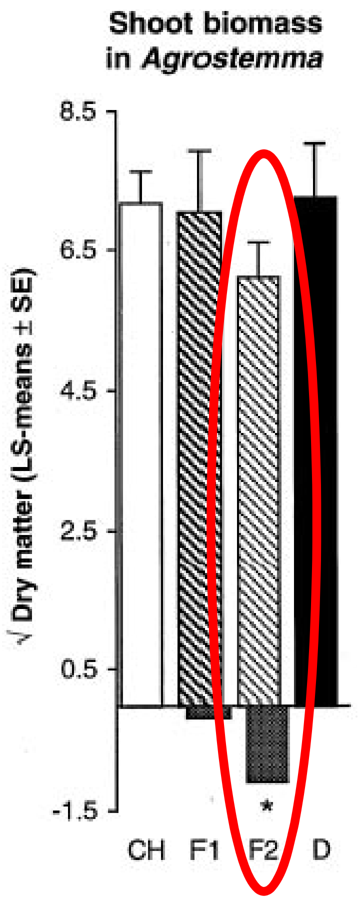


Fig. 4. Shoot biomass of *Agrostemma githago* parents and the hybrid line from crossings with a population from Hesse, central Germany. The bars at the bottom line are deviations from the expected values (*$P < 0.05$). Abbreviation of provenances and crossing design as in Fig. 1.

Keller, M., Kollmann, J., Edwards, P.J. (2000) Journal of Applied Ecology 37, 647-659

Outbreeding depression

Hybridisation with introduced populations can reduce the fitness of still existing local populations

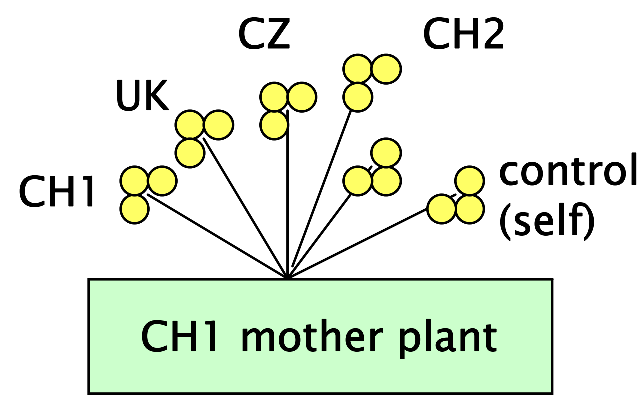
Mechanisms: *dilution of local adaptation*, disruption of beneficial epistatic genetic effects (*hybrid breakdown*)

Hybrid breakdown often only visible in the F2 or later generations (in the F1 masked by "heterosis")

3. The provenance question: outbreeding depression

Hybridisation experiment on *Plantago lanceolata*

Evidence for outbreeding depression not always very strong, phenomenon not very well studied in plants, need for further research

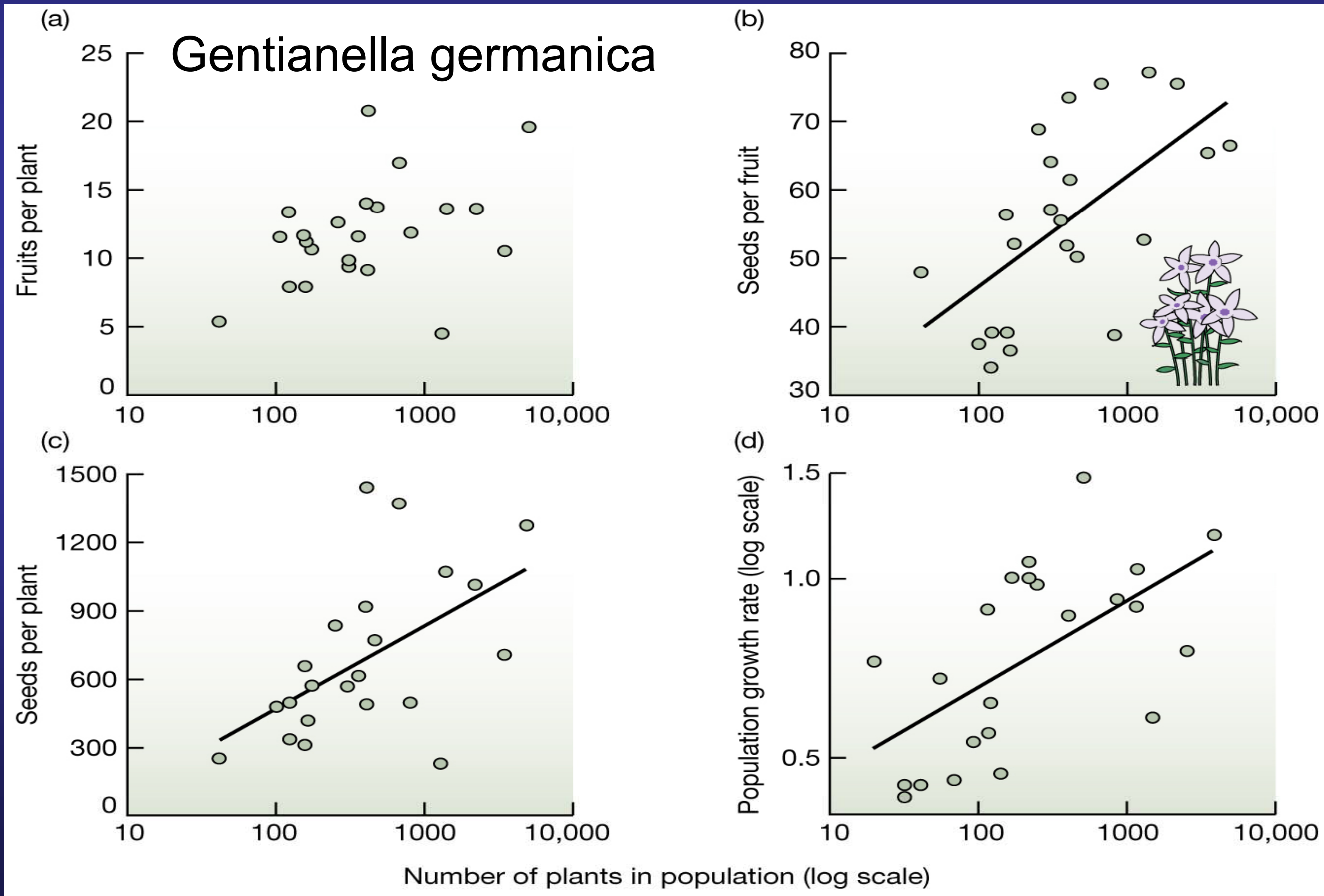


	CH2	CZ	UK
Early growth	↓ F1, F2	0	↓ F2
Biomass	0	0	0
Seed production	0	↑ F2	0

Crémieux et al., Am. J. Botany, in revision

4. Genetic diversity: bottlenecks and inbreeding

Much evidence for inbreeding depression: reduced fitness of small populations, in outcrossing species even in populations of more than 1000 individuals



Townsend et al. 2008, adapted from Fischer & Matthies (1998)

4. Genetic diversity: bottlenecks and inbreeding

Genetic diversity has to be considered at 2 levels

1. Genetic diversity of the source population (proxy: size)

2. Genetic diversity of the restored population (proxy: number of seed families collected and established)

(3. Losses of genetic diversity if propagated in stock for multiple generations)

There is a trade off between local adaptation and genetic diversity!

Small locally adapted populations may suffer from inbreeding depression. „Genetic refreshment“ by introducing non-local populations may remove inbreeding depression but also reduce local adaptation (or provoke outbreeding depr.)

4. Genetic diversity: effects independent of inbreeding

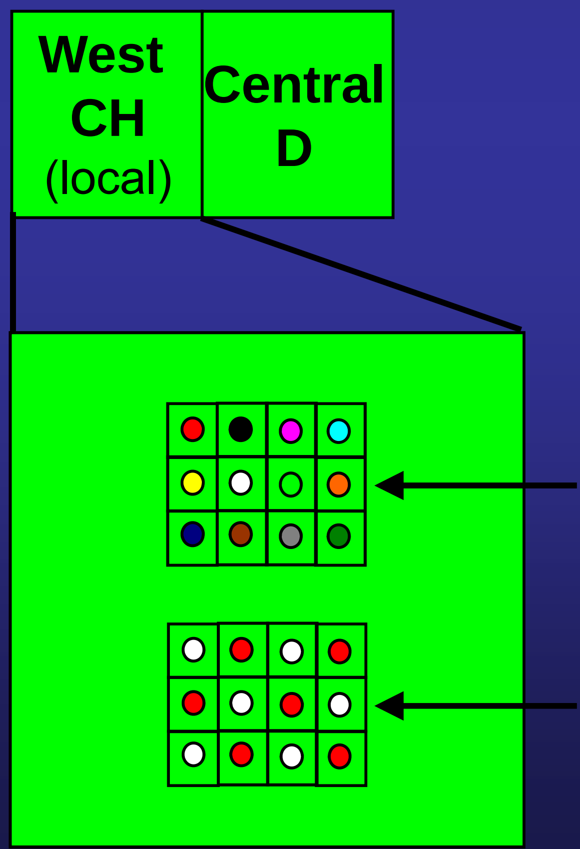
Niche complementary effects of inbreeding

System: wildflower strips

Test species: *Echium vulgare, Cichorium intybus, Origanum vulgare*

2 provenances, 8 blocks

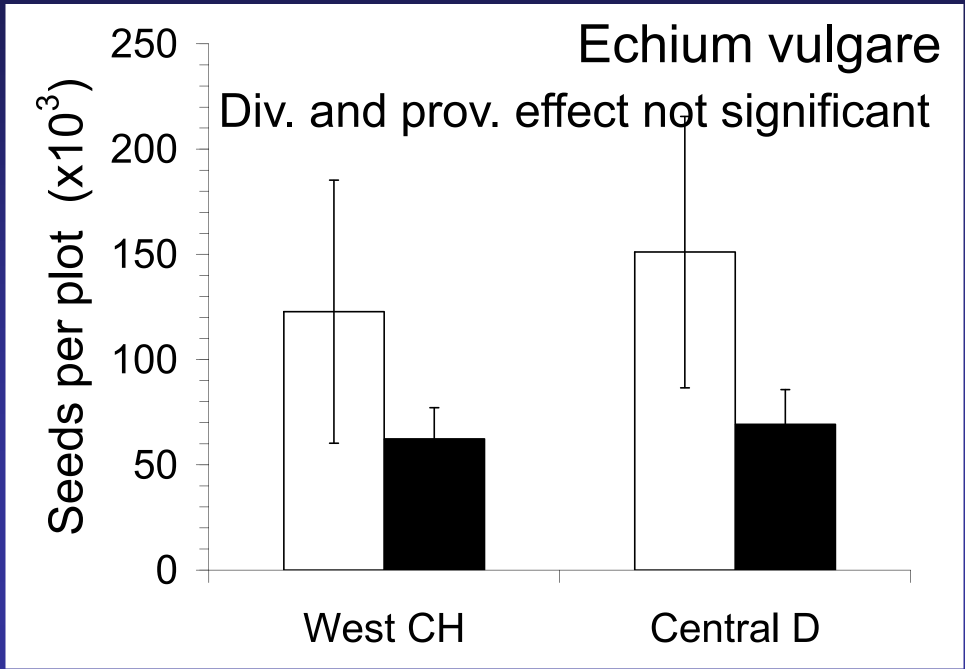
Test of genetic diversity effects



<u>High diversity</u>: each individual from a different mother

<u>Low diversity</u>: 12 plants from only two different mothers

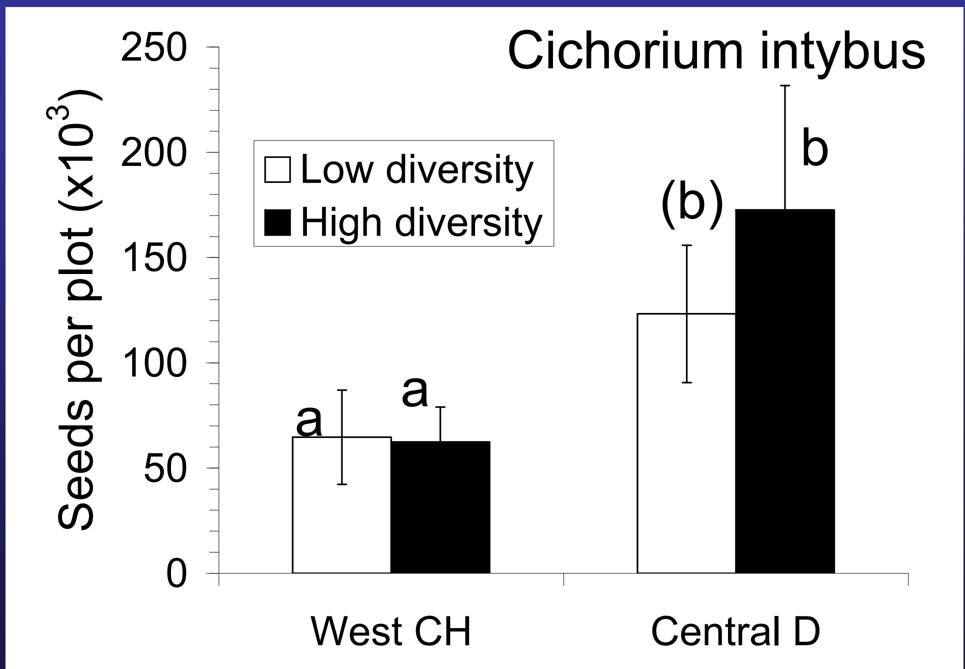
4. Genetic diversity: effects independent of inbreeding

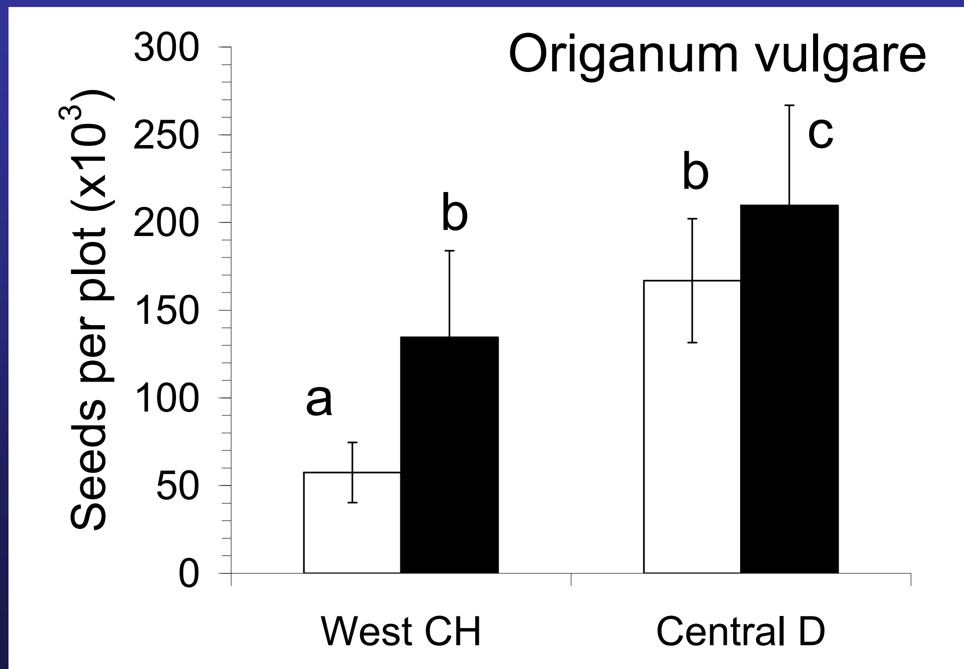


Magnitude of diversity effect nearly as large as that of prov. effect

Due to large scatter diversity effect only significant in one species: higher divers. → higher productivity

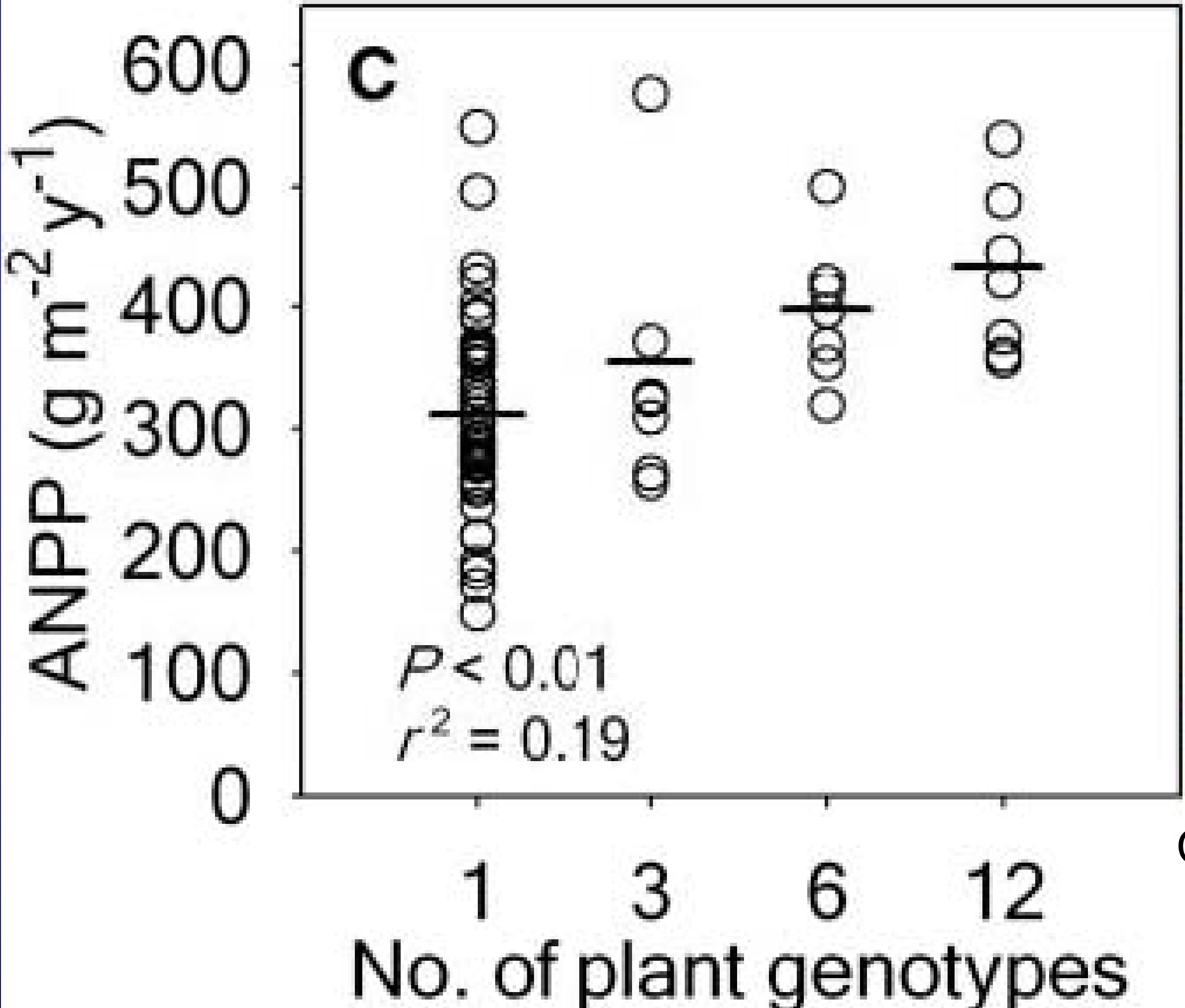
Bischoff et al. 2009, Rest. Ecol (online)





4. Genetic diversity: effects independent of inbreeding

Confirmed by several other studies but quite recent research topic, difficult to evaluate the importance



Crutsinger et al. 2006, Science

5. Conclusions: Facts to be considered in restoration

- Local genotypes are on average superior: risk of maladaptation and failure in establishment if non-locals are used
- Habitat matching may be more important than geographical distance in deciding what is local (further research on scales of adaptation required)
- There is evidence for an invasiveness of superior introduced genotypes which may be more detrimental than maladaptation (lack of knowledge)
- The introduction of non-local genotypes changes interactions with organisms of other trophic levels and has an impact on the ecosystem
- Outbreeding depression may reduce the fitness of existing local populations but inbreeding effects seem to be stronger
- A sufficient diversity of the source and the restored population is important for restoration measures

5. Conclusions: continued and recommendations

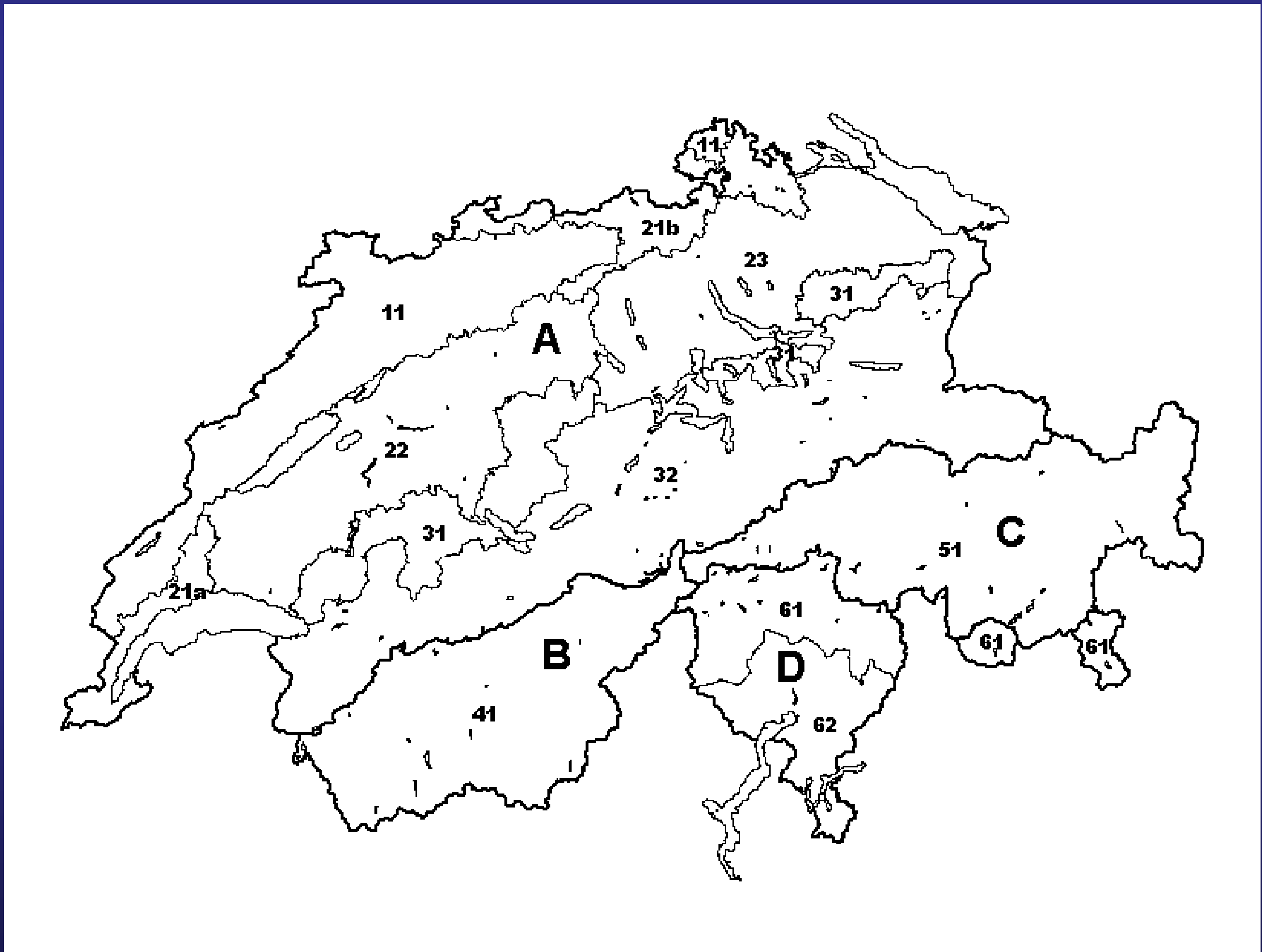
- There may be a trade off between high levels of local adaptation and a high genetic diversity

Recommendations: adapted from Van der Mijnsbrugge, Bischoff & Smith (in press), BAE

	Where to collect	How to collect	Transfer method and propagation
General rules	- Collect locally - Match habitat as closely as possible	- Sample at least 50 individuals per source population, record the number and location - Collect preferably one population, mix different source populations if they are too small or inbred	- Choose an appropriate transfer method considering conservation value and amount of seeds required
First approach: areas of high conservation value, reintroduction of rare plants	- Collect from closest source populations - Collect from same habitat type	- Record size of the source population and/or determine degree of heterozygosity to identify need for population mixing	- Transfer directly without propagation, e.g. hay strewing, brush harvesting or manual transfer
Second approach: areas of low conservation value, restoration of industrial/agricultural sites, grasslands, reforestation, requiring large amounts of seed	- Collect from populations of the same seed zone, based on climate and geomorphology - If possible, refine seed zones by considering life history traits and genetic structure of source populations	- Collection of several source populations often not avoidable to obtain sufficient amounts of seed but keep them separate and respect general rules (see above)	- Propagate collected seeds and replenish stock at regular intervals to prevent genetic drift - Avoid seed or seedling selection during propagation and transfer

5. Conclusions: delineation of seed zones

Seed zones in Switzerland: Seed transfer only allowed within 4 main bio-geographical regions; for rare species showing strong geographical differentiation 11 sub-regions are defined



A Jura, Midlands and Northern (Pre-)alps

B Western central Alps

C Eastern central Alps

D Southern alps

Gonseth et al., 2001, in SKEW 2003

5. Conclusions: genetic diversity

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Thanks for your attention!

Danke schön an:

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