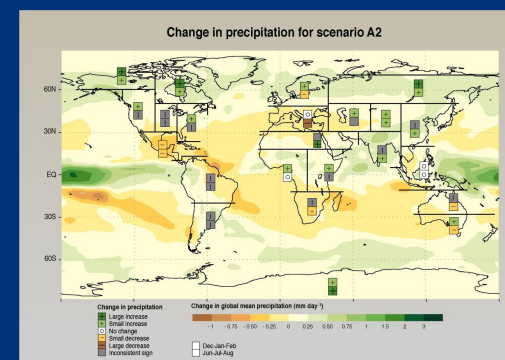
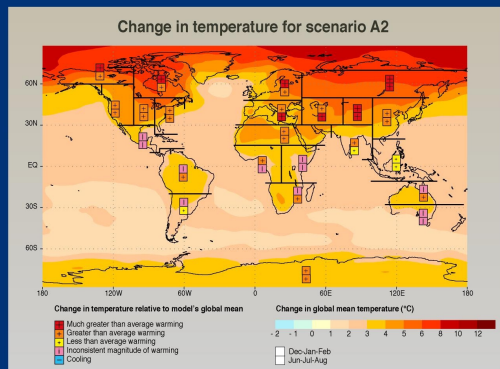


The trailing edge: genetic implications

Bruno Fady
INRA – URFM, Avignon, France



IPCC
INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE



IPCC
INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE



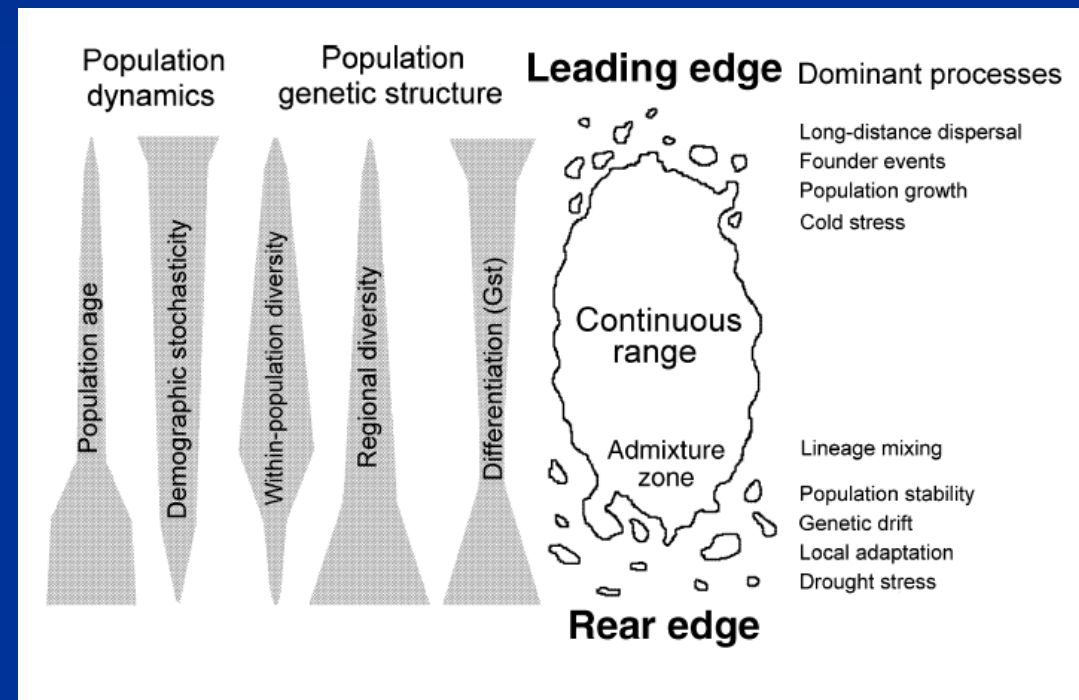
EvoTREE SEA workshop
Sopron, Hungary, 11-14 May 2009



The trailing edge: genetic implications

What is the trailing edge?

- A notion of movement
- Evolutionary history perspective:
Depends on the stage (interglacial or glacial)



The trailing edge: genetic implications

What is the trailing edge?

- A notion of movement
- Evolutionary history perspective:
Depends on the stage
(interglacial or glacial)
- Global change perspective:
Anywhere (land use change)

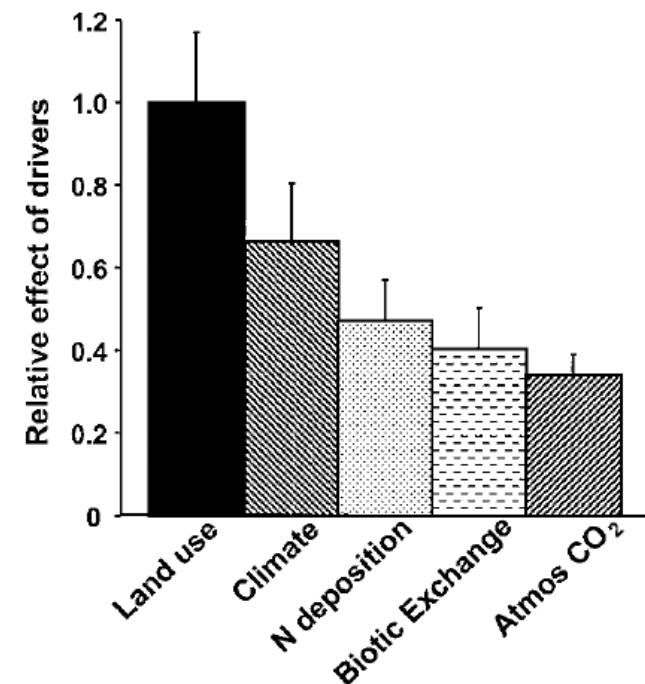


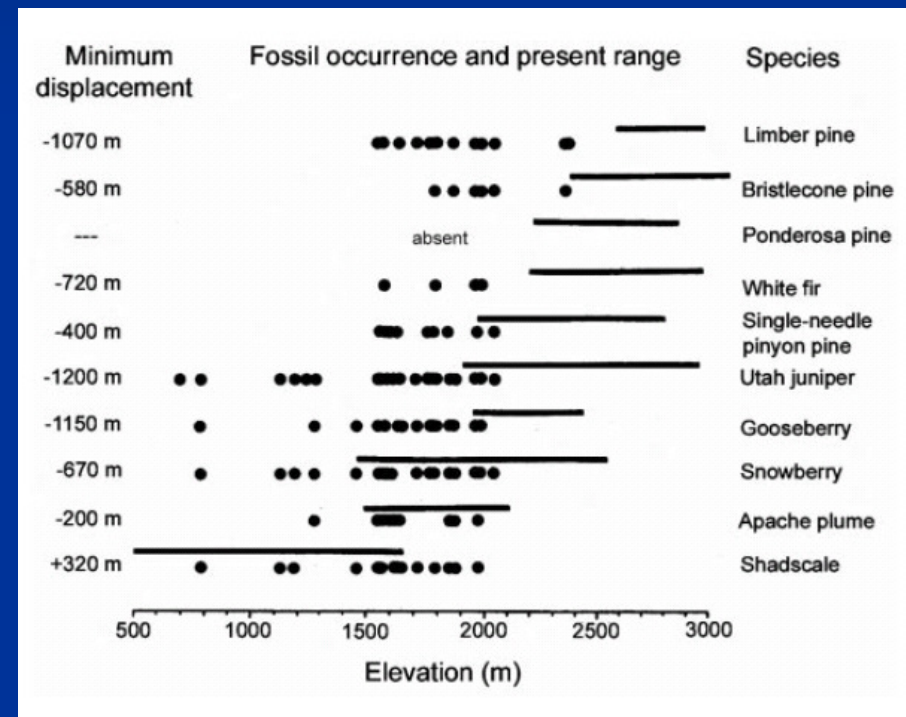
Fig. 1. Relative effect of major drivers of changes on biodiversity. Expected biodiversity change for each biome for the year 2100

Sala et al. Science 2000

The trailing edge: genetic implications

What is the trailing edge in the Climate change perspective?

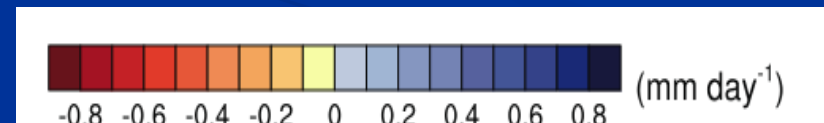
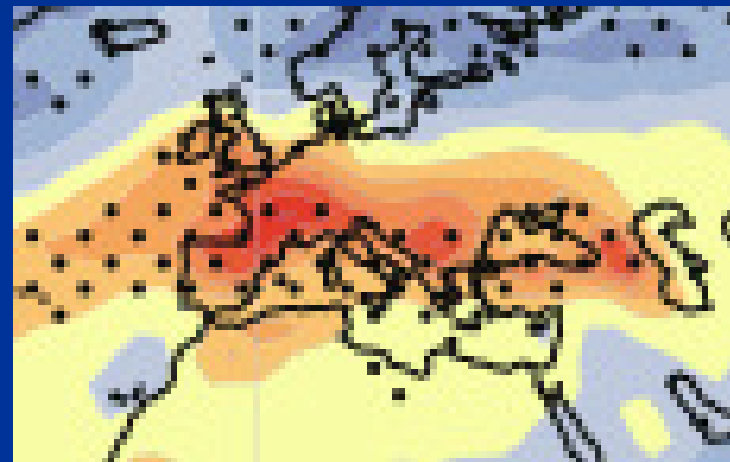
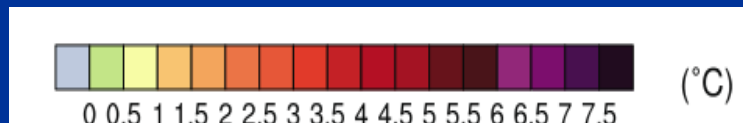
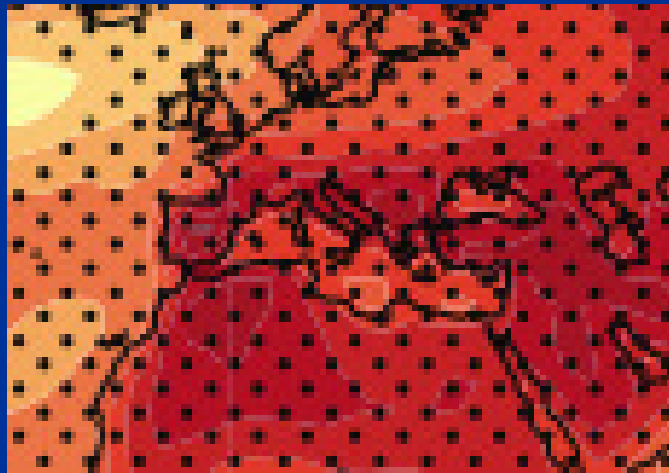
- Low latitude (locally low elevation) margins of distribution ranges
- But also trapped warm species that will move downward from mountains and southwards from higher latitudes



Elevation ranges of 10 woody plants from Nevada mountains during the last glaciation (dots) and current (lines). Amount of elevation change and direction are different for each species. *Davis & Shaw Science 2001*

Receding edge scenario in Europe

= = increased *summer drought*
(+3 to 5 °C; -0.1 to -0.4 mm/day)!



=> Consequences on survival and
distribution of species and ecosystems

The trailing edge: genetic implications

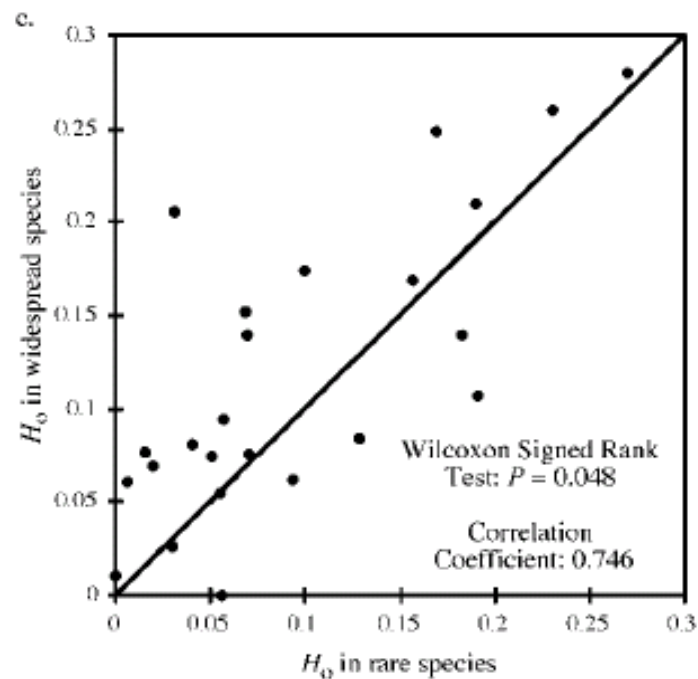
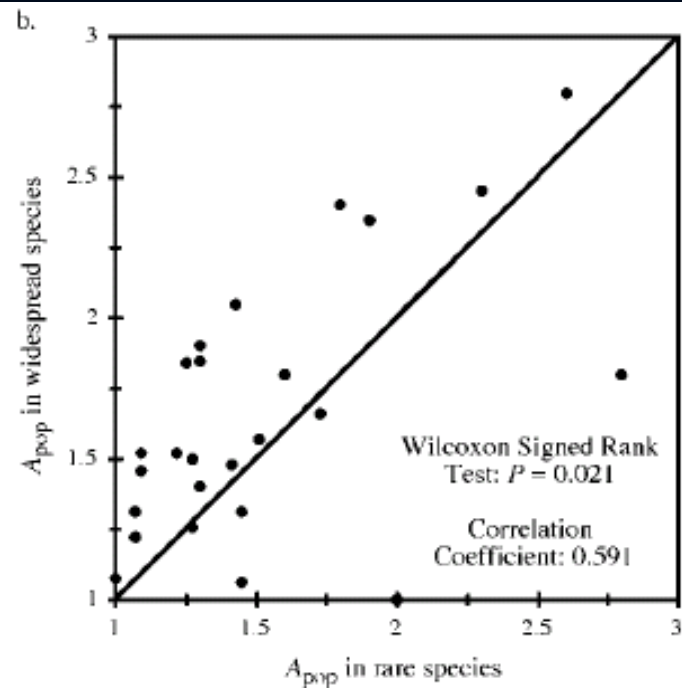
Trailing edge populations (*e.g.* as opposed to leading edge) have not yet received much attention per se, although species range margins have. Two main genetic features are usually identified that limit species ranges:

- Low genetic diversity, *i.e.* low potential for selection to generate local adaptation.
- Significant gene flow from core populations, bringing mal-adapted genes to range margins.

The trailing edge: the argument for low genetic diversity

Argument 1: populations at the margins of a species distribution area are less genetically variable than core populations, because of low population density, patchy distribution and, thus, genetic drift (e.g. Young et al. 1996). Hence, differentiation is high between central and peripheral populations.



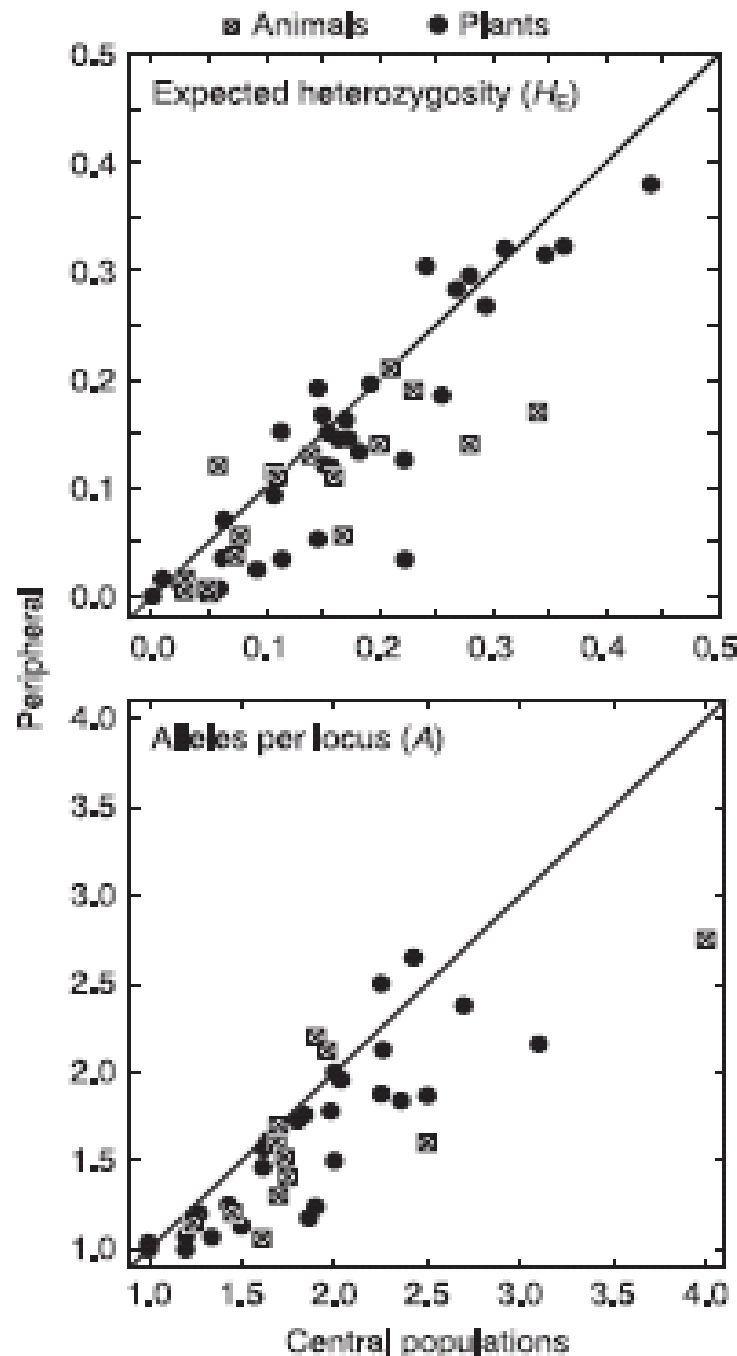


Extending the approach: rare vs widespread species

-Within population genetic diversity of rare and widespread congeners is phylogenetically conserved

-Rare species tend to have slightly less genetic diversity (but not more differentiation) than their widespread congeners (34 species pairs investigated)

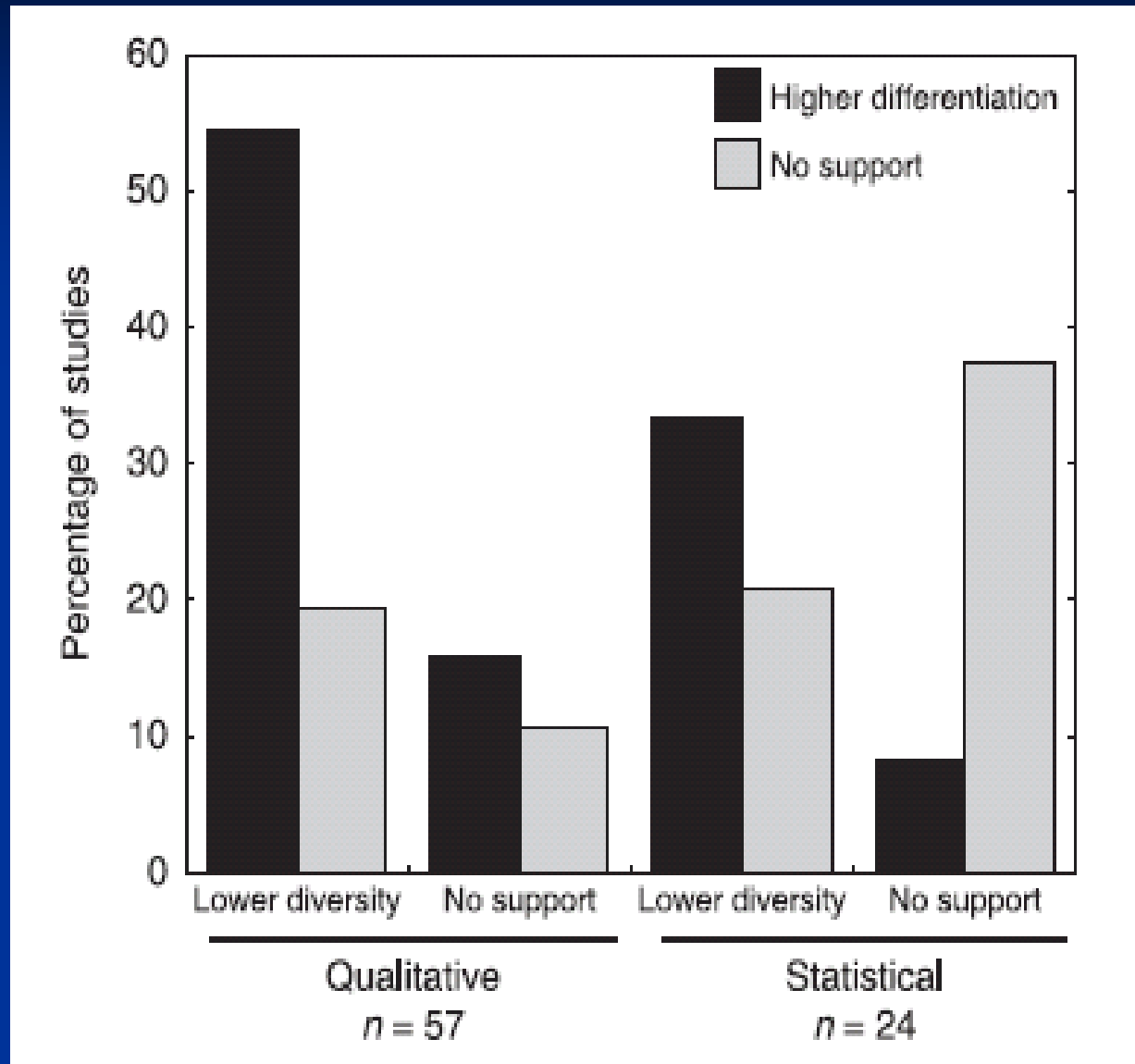
Gitzendanner & Soltis (Am. J. Bot.) 2000



Marginal vs core populations

64 per cent of 134 published studies (115 species) detect a decline in within-population genetic diversity towards range margins

Eckert et al. (Mol Ecol) 2008



Marginal vs core populations

70 per cent of 134 published studies (115 species) detect an increase in among-population genetic differentiation towards range margins

Genetic diversity of trailing edge populations (species)

“Eckert et al. (2008) document that 64 per cent of 134 published studies detected a decline in within-population genetic diversity, and 70 per cent an increase in among-population genetic differentiation, towards range margins using nuclear molecular genetic markers. In most cases, however, the difference in genetic diversity between central and peripheral population was not large....

... And most studies deal with species having undergone recolonization (and thus bottlenecks) during the Holocene...

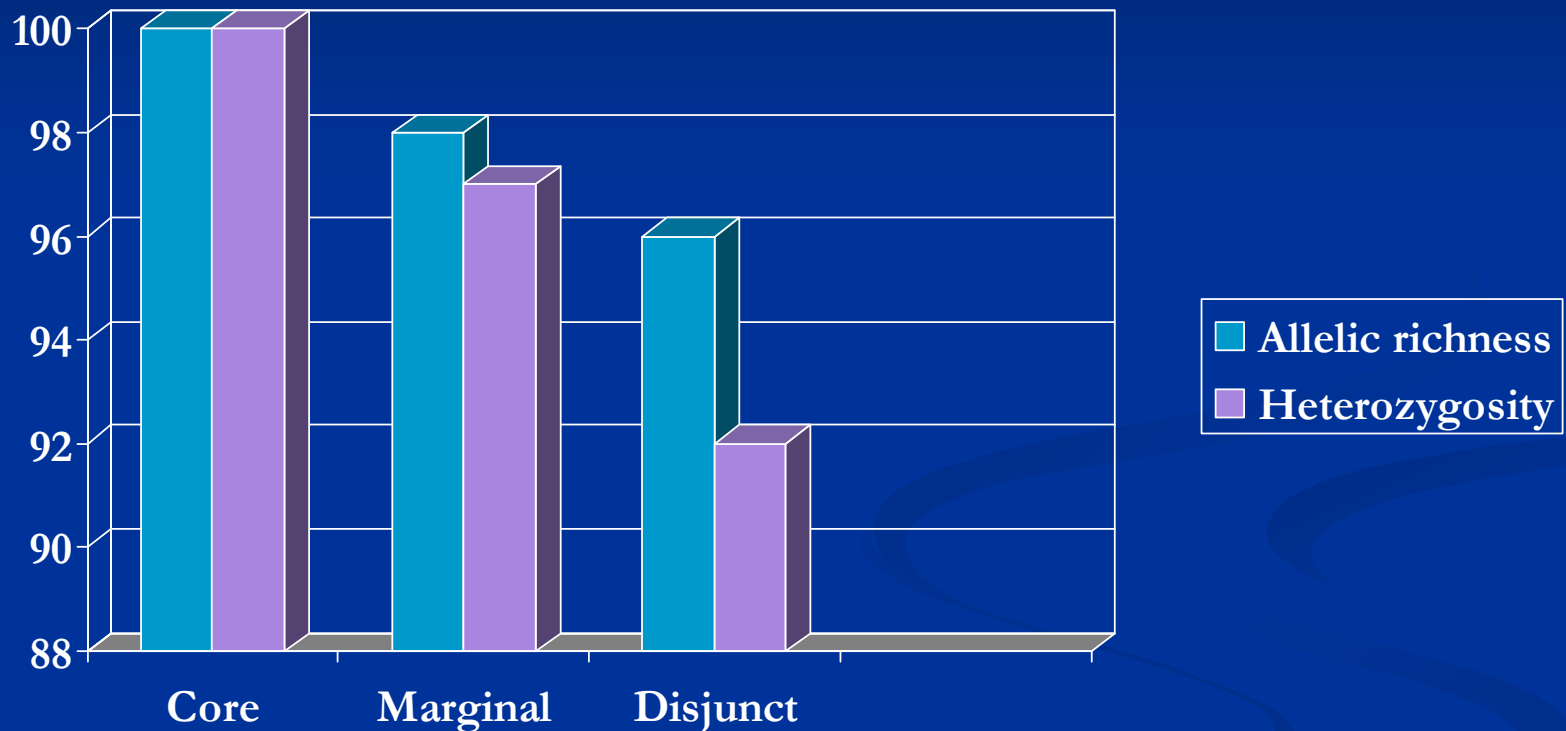
... Thus gene flow between core and periphery must be substantial...”

Genetic diversity of trailing edge populations (species)

On average, marginal populations (*Eckert et al. 2008*) and rare species (*Gitzendanner & Soltis 2000*) display slightly lower gene diversity and higher (or similar) differentiation than core populations and widespread species ==> genetic drift and differentiation to some extent at range margins.

Patterns of marginality, life history traits and evolutionary history in general may affect this general but weak trend: higher diversity in marginal vs disjunct populations (*Aitken & Fady in prep*), in stable vs trailing rear edge populations (*Hampe & Petit 2005; Fady 2005*), in trees than in animals (*Conord & Fady in prep*).

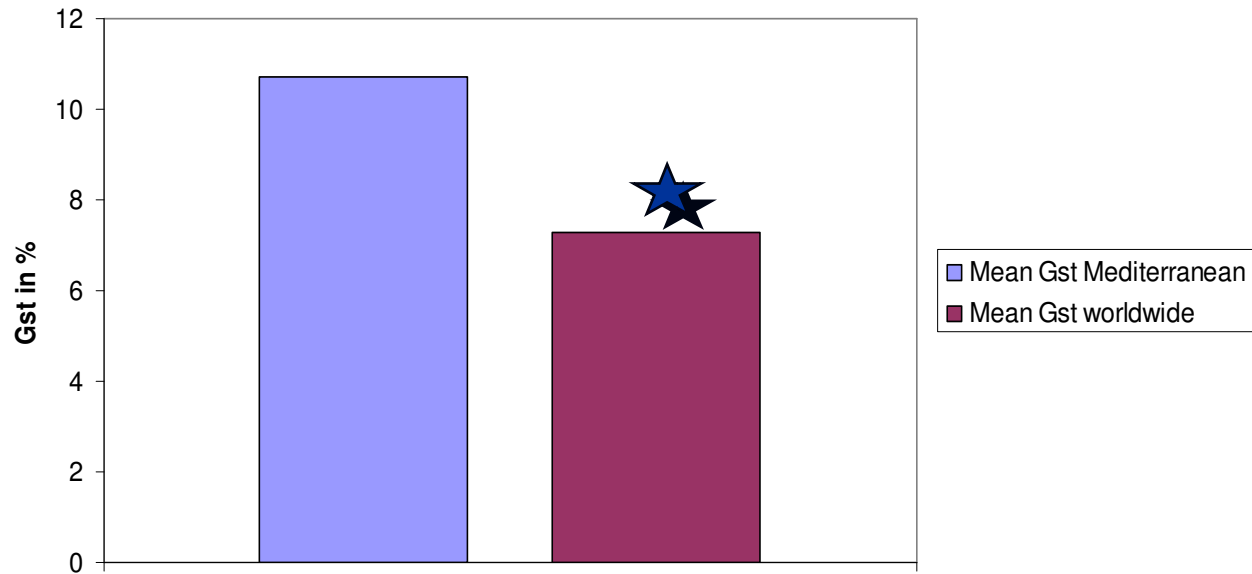
Type of marginality effects gene diversity: disjunct vs marginal populations



Genetic diversity decreases more in disjunct populations than in marginal populations in reference to central populations.

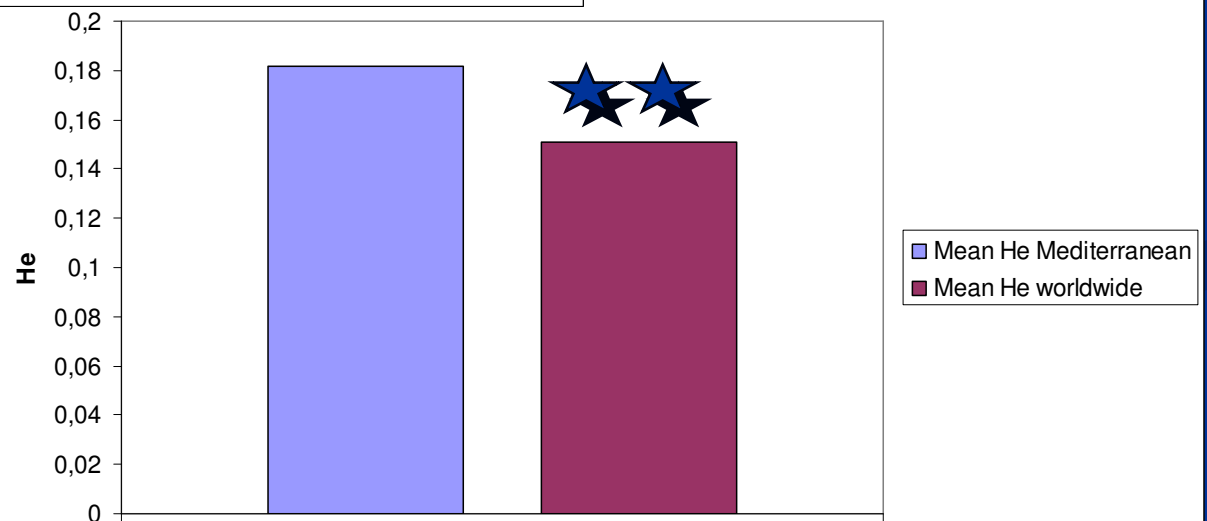
Aitken & Fady (in prep) 35 species in *Pinaceae*, 4 in *Cupressaceae*, 1 *Taxaceae* North America and Europe.

Stable rear edge populations have higher gene diversity

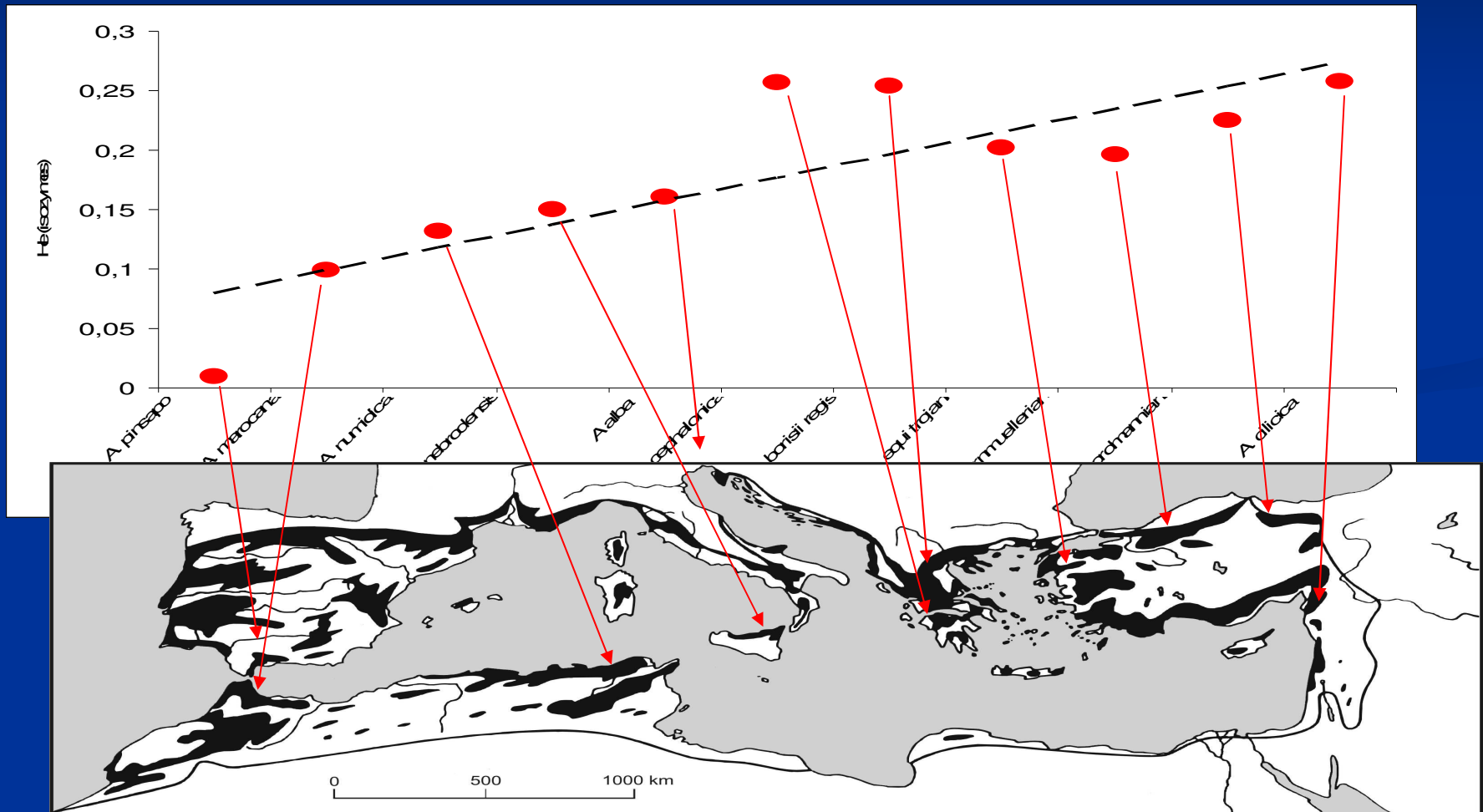


Mediterranean (refugial) conifers have more gene diversity within and among populations than conifers worldwide

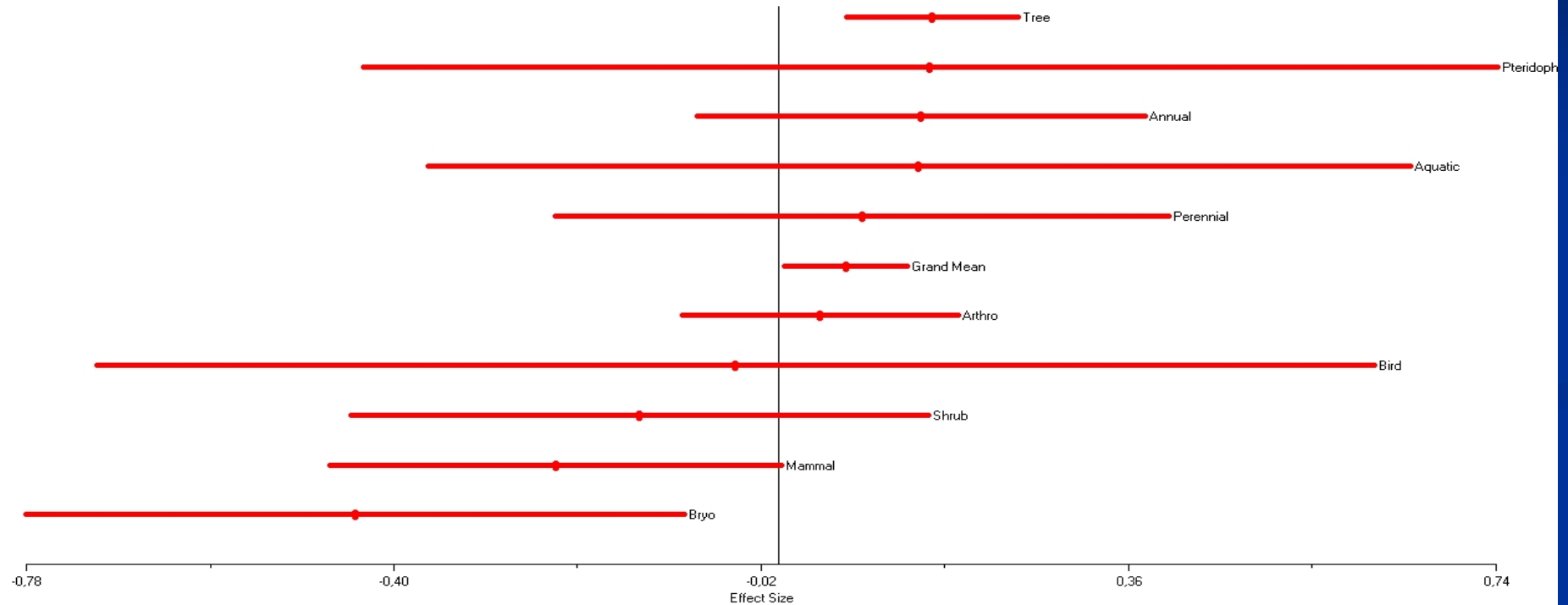
Fady (Taxon) 2005



Genetic diversity in rear edge populations is spatially organized in the Mediterranean refugial zone



Organization of genetic diversity of trailing edge populations depends on their life history.



A biome wide meta-analysis of more than 5000 Mediterranean population studies: effect of longitude (past climate) varies according to life history traits.

Conord & Fady, in prep

The trailing edge: genetic implications

There is not always reduced gene flow (high differentiation) and genetic drift (low diversity) in peripheral populations (*Eckert et al. 2008*).

Peripheral populations may not be characterized by low demographic values, more by high population density variability (*Gaston 2009*).

Peripheral populations may contain enough diversity for evolution to act through selection. They are evolvable?

The trailing edge: the argument for adaptation

Argument 2: Peripheral rear edge populations do not hold any evolutionary interest (/ do hold an evolutionary interest) for adaptation to climate change.

- Non-existent gene flow from better adapted populations / species: gene flow not an option for local adaptation (except in the form of interspecific gene flow, i.e. hybridization). Provided that population density remains over a threshold, the lack of gene flow should increase local adaptation.

- Potential maladapted gene flow from higher latitude (elevation) populations (gene swamping) very probable if trailing edge populations are not isolated (disjunct).

The trailing edge: the argument for decreasing genetic diversity over time as climate change

Under climate change, populations at the trailing edge of a species distribution area should become less genetically variable as population density becomes lower over time (genetic drift, consanguineous mating) and gene flow is reduced

The trailing edge: genetic implications

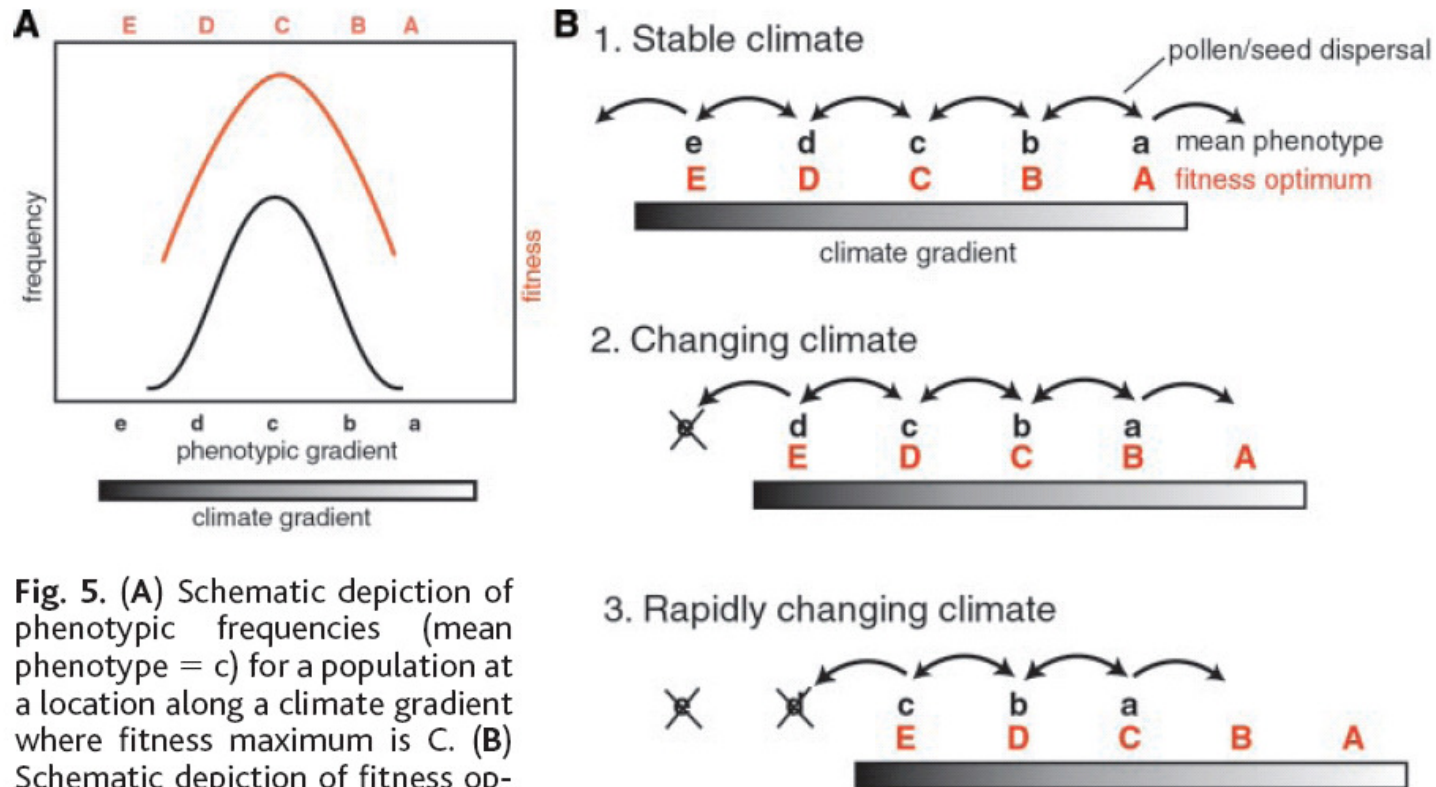


Fig. 5. (A) Schematic depiction of phenotypic frequencies (mean phenotype = c) for a population at a location along a climate gradient where fitness maximum is C. (B) Schematic depiction of fitness optima (red) for a species that ranges across a climate gradient. Adaptive differentiation of population phenotypes is shown in black; arrows indicate gene flow through pollen and seed dispersal. Spatial distributions of the climate gradient, fitness optima, and phenotypic frequencies are shown for three conditions: 1, stable climate; 2, slowly changing climate; and 3, rapidly changing climate.

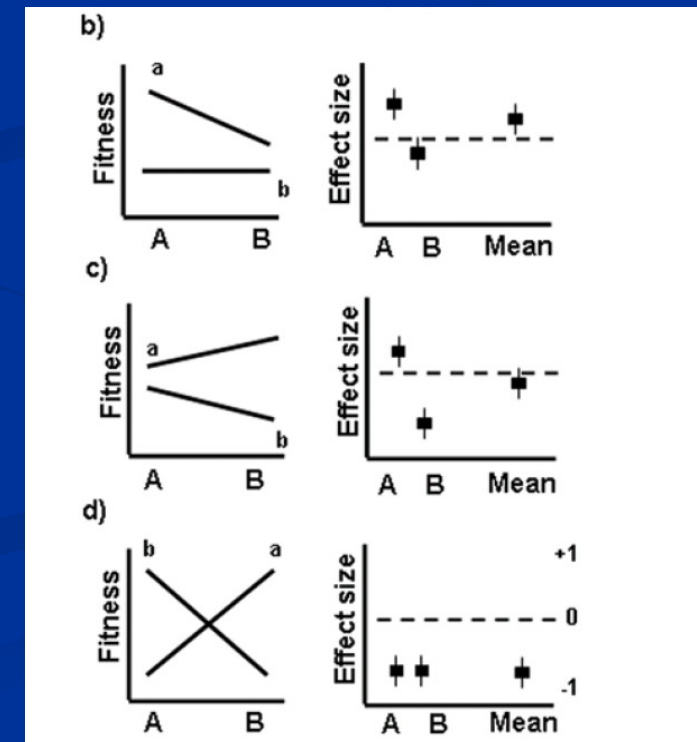
***An example of population density decrease at the trailing edge
in the French Alps***



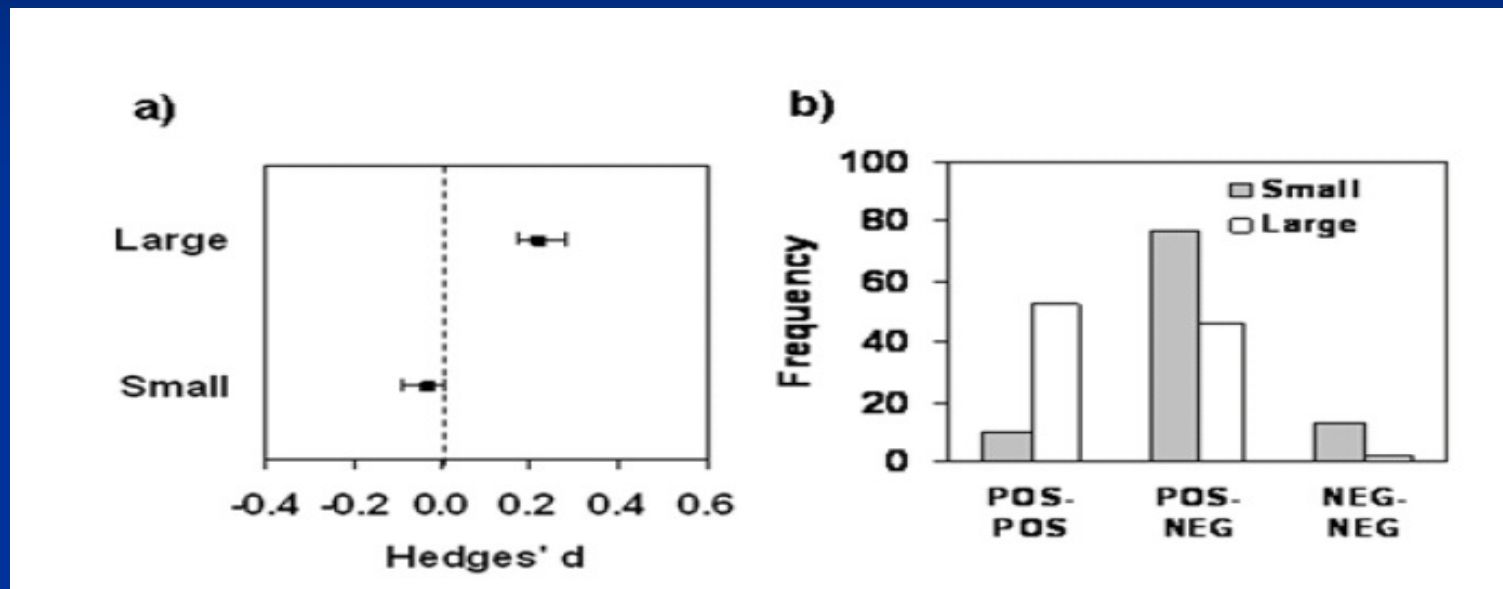
Abies alba dieback after the 2003 summer heat wave, southern France (Mont Ventoux, elevation 1200 m).

Are plants locally adapted? A meta-analysis of local adaptation in plants.

“Local plants performed better (reproductive success, plant size, survival, germination) than foreign plants at both sites (a) of a pair-wise comparison (strict definition of local adaptation) only in 45.3% of the 1032 compared population pairs (32 species) ...”

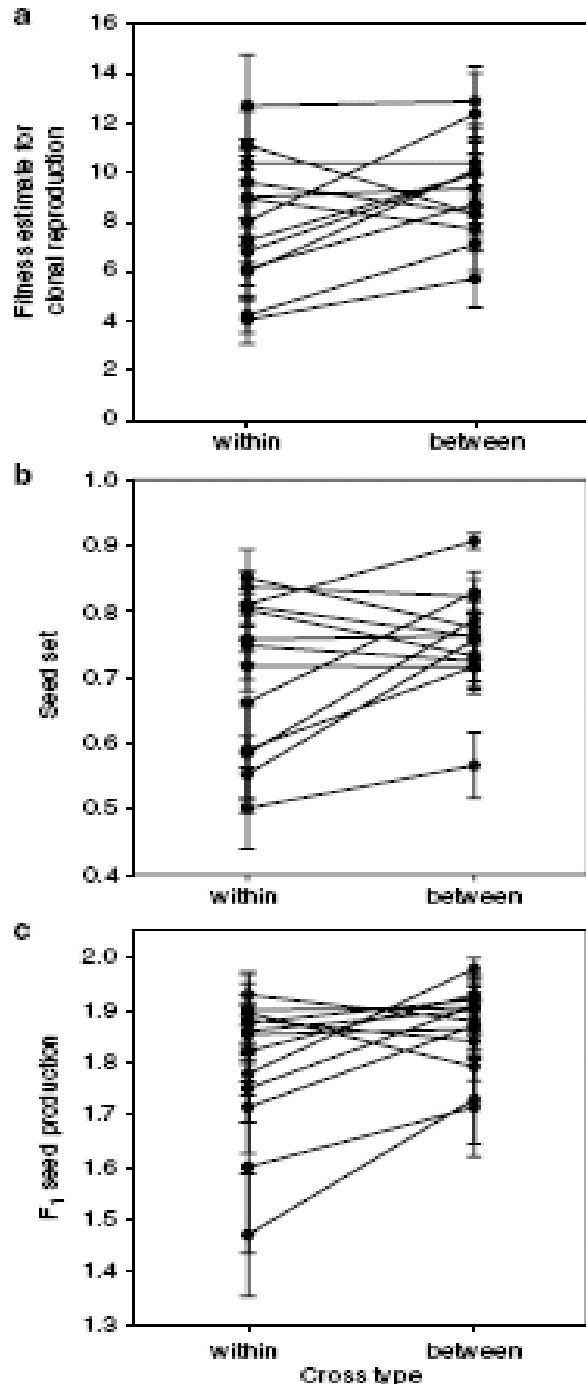


***Local adaptation may be rare at the receding edge.
Evolvability towards climate change unlikely because of
inefficient selection***

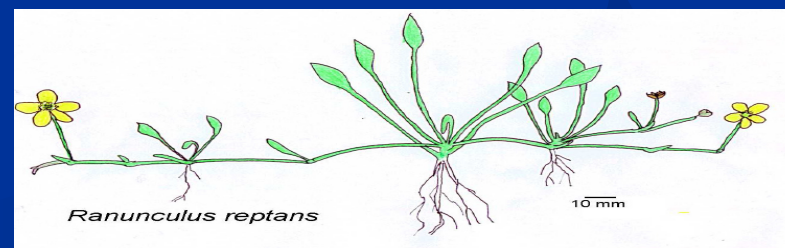


“ ... Furthermore, we found local adaptation much more common for large plant populations (>1000 flowering individuals) than for small populations (<1000 flowering individuals) for which local adaptation was very rare.”

Gene flow can promote local adaptation at the receding edge

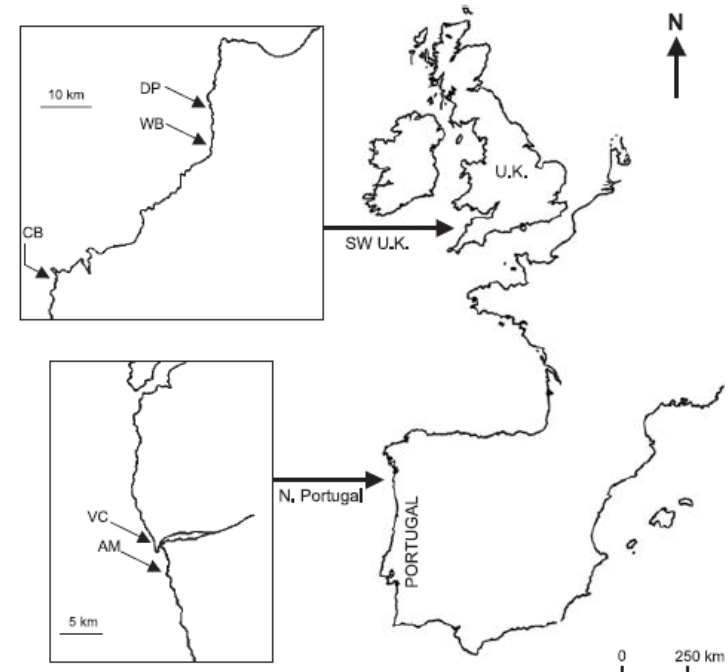
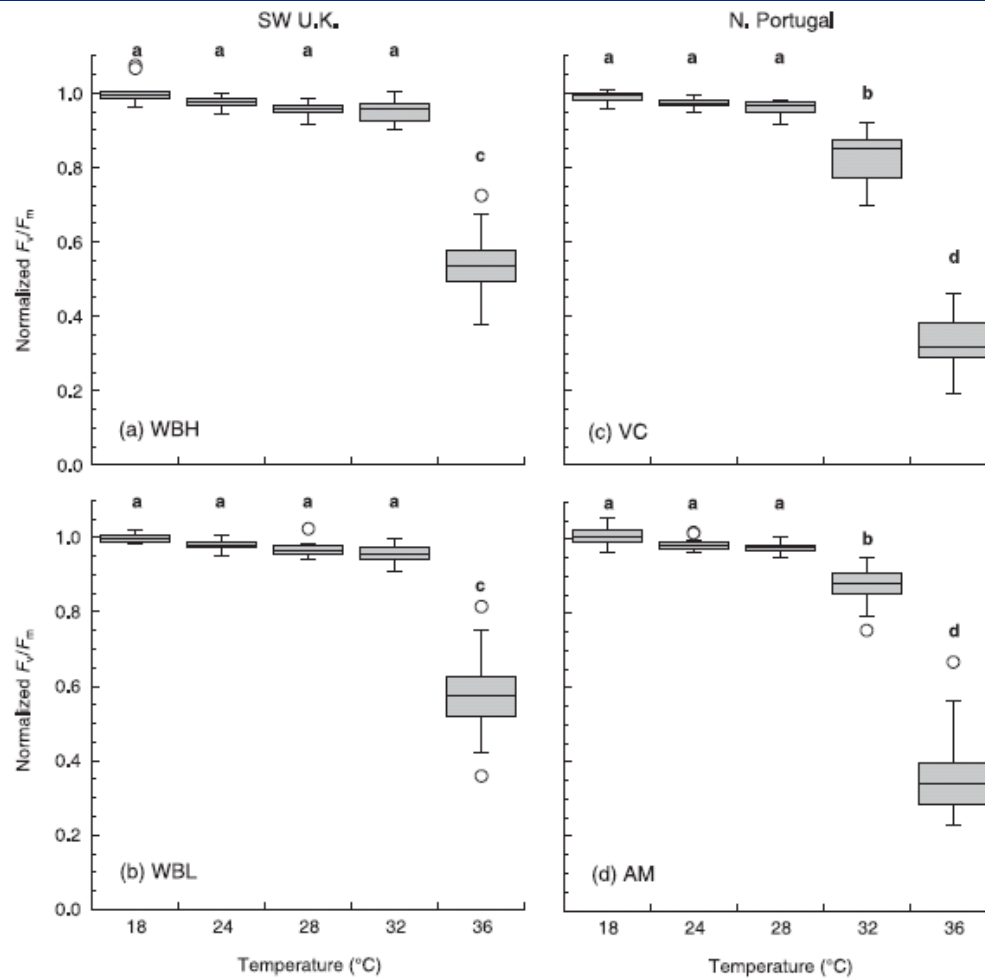


Theory and experimental evidence suggest that small populations have reduced fitness because of increased inbreeding depression, drift load and reduced mate availability. Genetic rescue may come from outbreeding gene flow.



Willi & Fischer (Heredity) 2005

Trailing edge populations of the intertidal seaweed *Fucus serratus* are least adapted to temperature increase

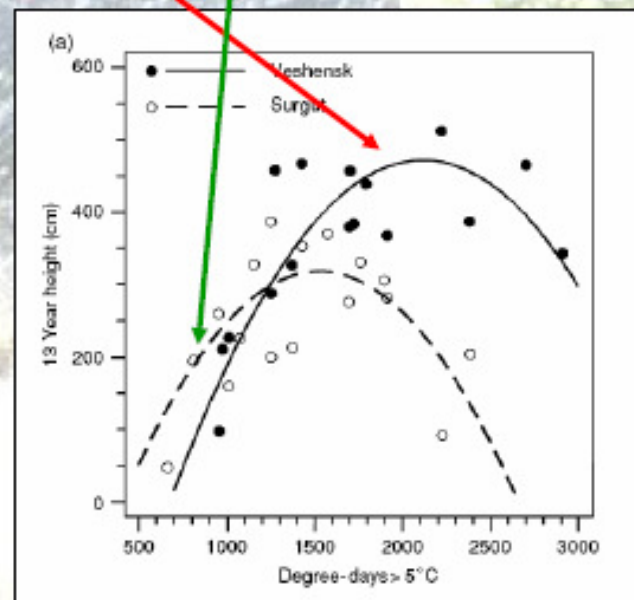
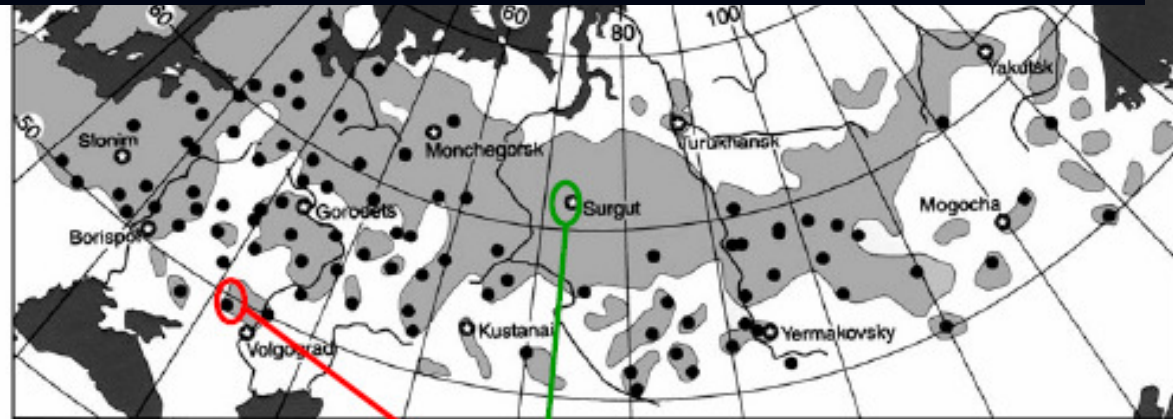


Less resilience to heat shock at the trailing edge

Trailing edge populations may harbor increased phenotypic plasticity towards global warming than core or leading edge populations

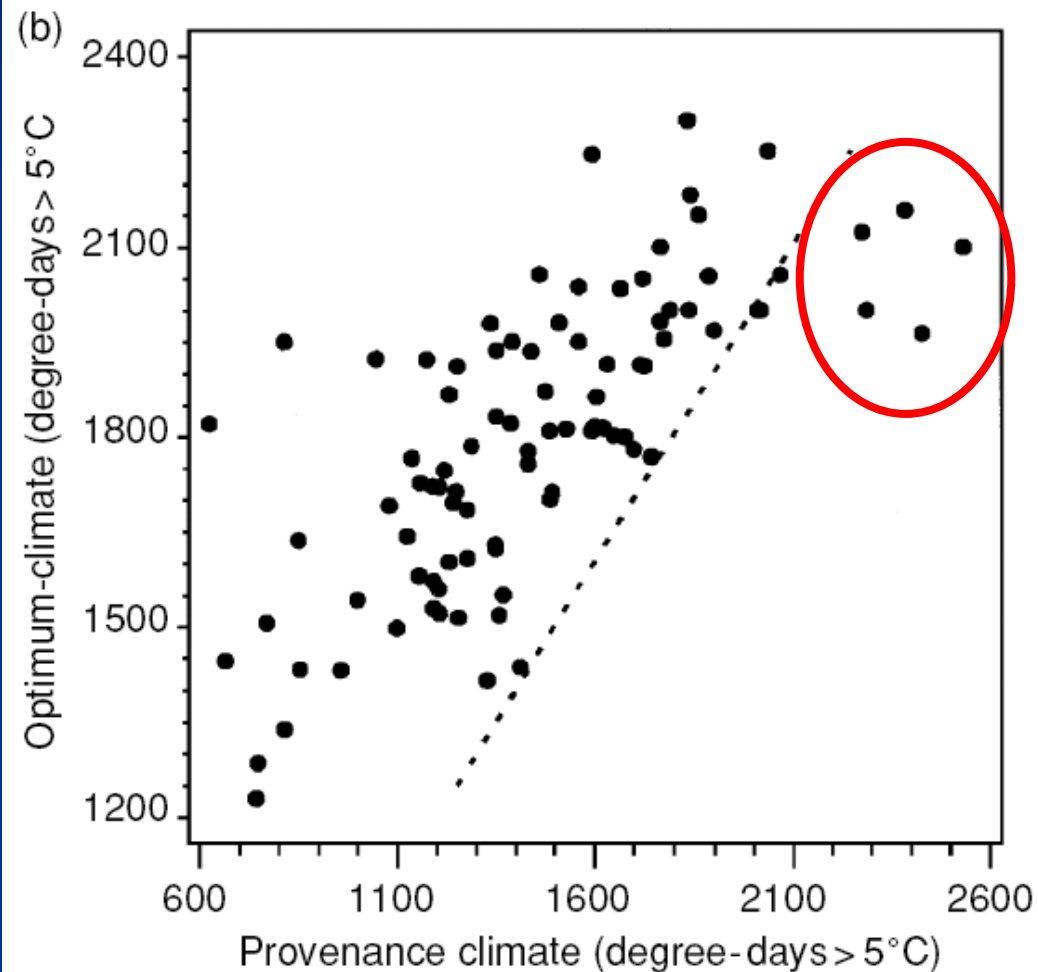
Southern rear edge provenances of *P. sylvestris* show a better response to increased temperature than northern ones.

Rehfeldt et al.
(Glob Change Biol) 2002



Trailing edge populations may harbor increased phenotypic plasticity than core or leading edge populations

Southern rear edge provenances of *P. sylvestris* already inhabit a climate slightly warmer than their optimum. They might have little leeway to express their phenotypic plasticity towards increased temperatures



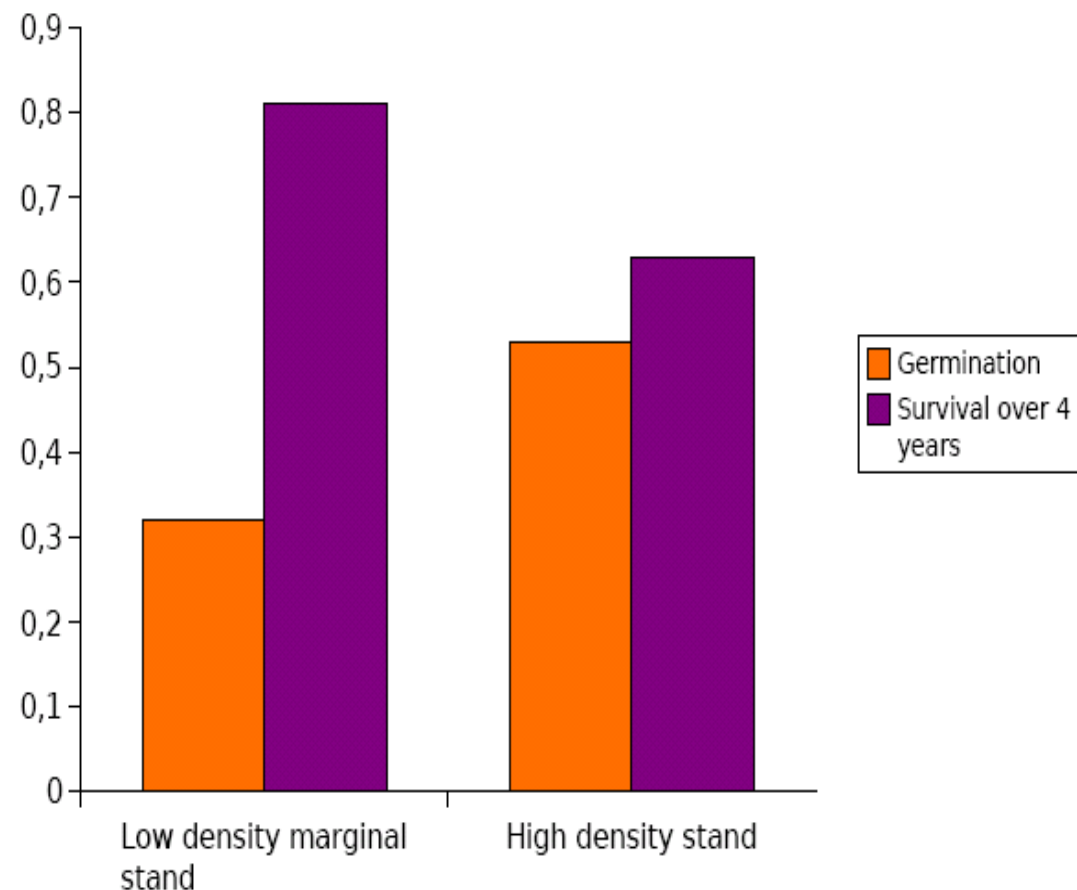
Lower population density decreases seed set and increases selfing events in *Abies alba* at the trailing edge.



However, overall fitness does not change and fitness of low density marginal stands is higher under stressful conditions (e.g. water stress) ==> genetic purge

Restoux et al. (Web Ecology) 2008

Germination and survival rates of seedlings



Lowering density increases selfing: an effect of the rear-edge

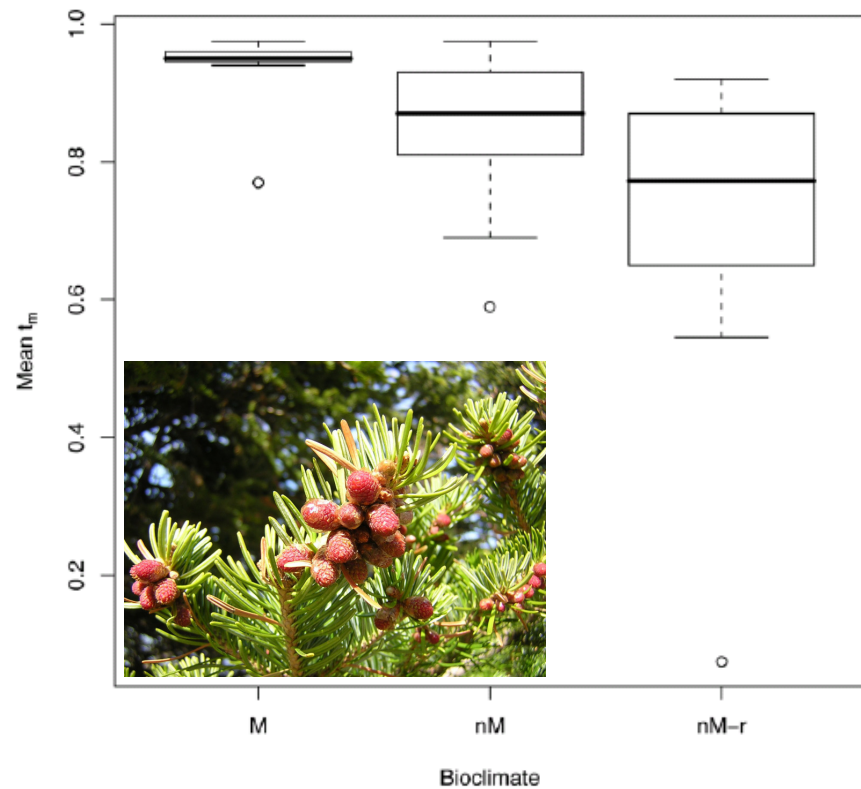


Fig. 2. Outcrossing rates over three bioclimates (Mediterranean, M, non-Mediterranean, nM, and rear edge non-Mediterranean nM-r) in *Abies*, *Picea* and *Pinus* species worldwide.

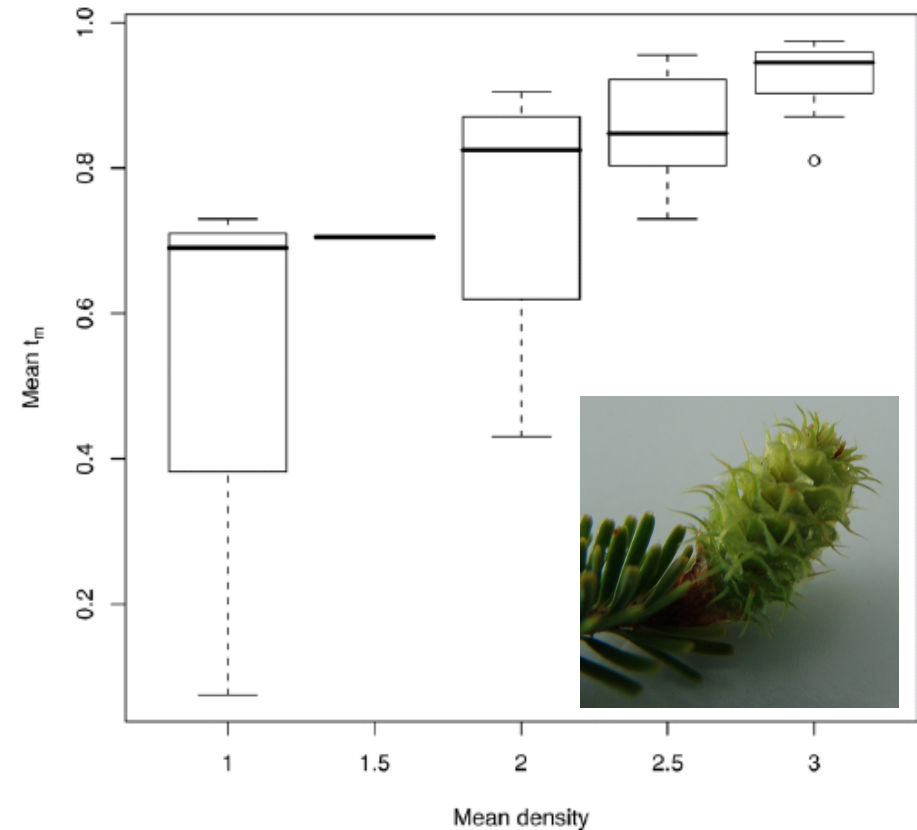
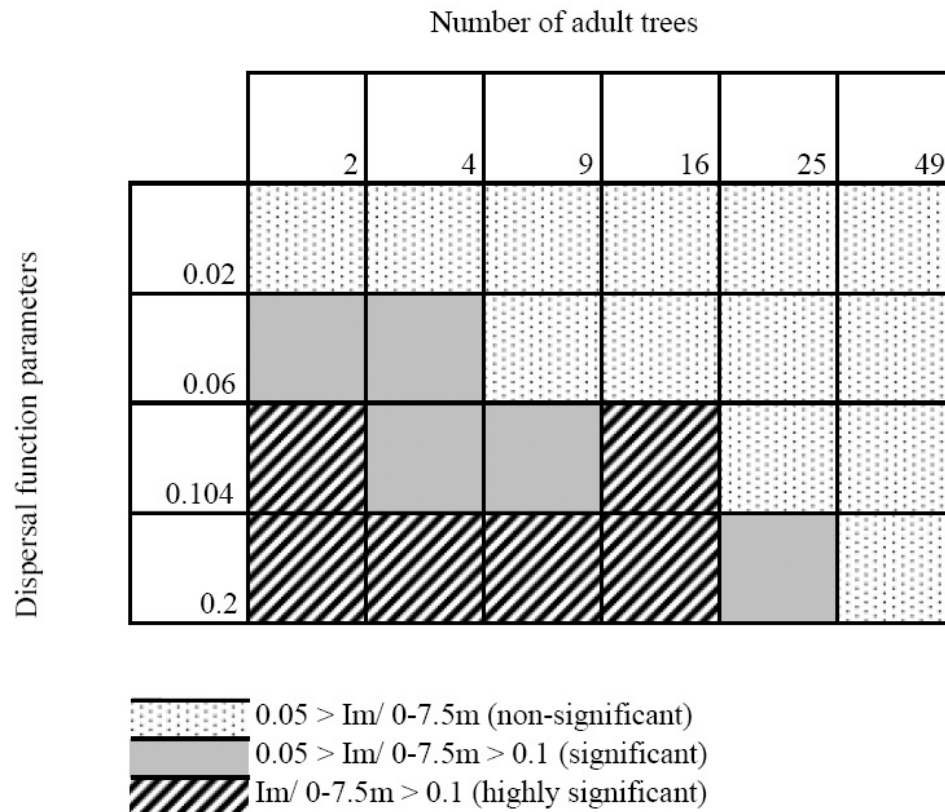


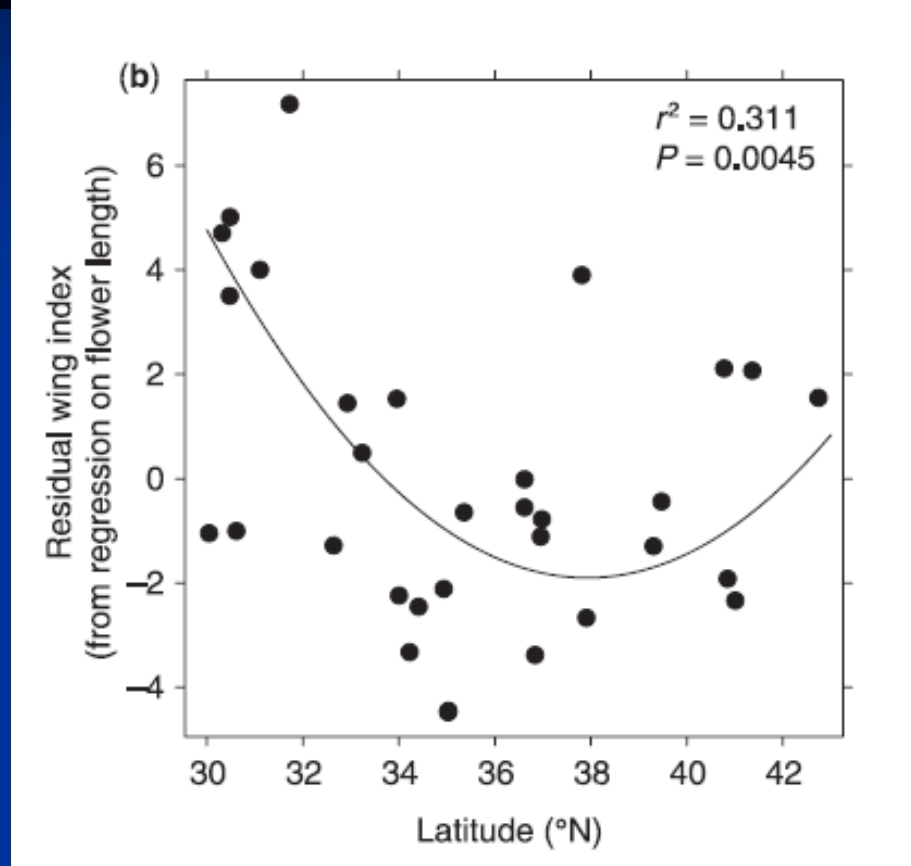
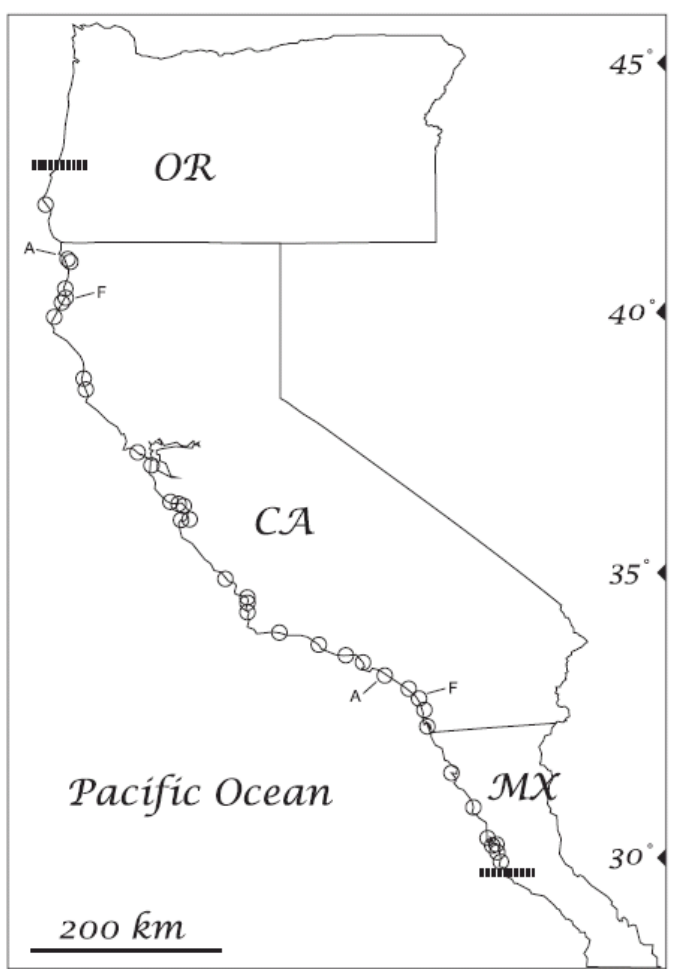
Fig. 3. Effect of density on outcrossing rate at the population level over three genera *Abies*, *Picea* and *Pinus*.

Effective adult tree density must be very low for random mating to be disrupted



Moran index for the first distance class simulated (0 – 7.5 m) for different adult tree densities and seed dispersal distances (dispersal mode).

Local adaptation may not be equally tested for all traits



Ability to disperse increases as populations near range edge in *Abronia umbellata*. Range is limited by gene flow.

The argument for hybridization as a rescue factor

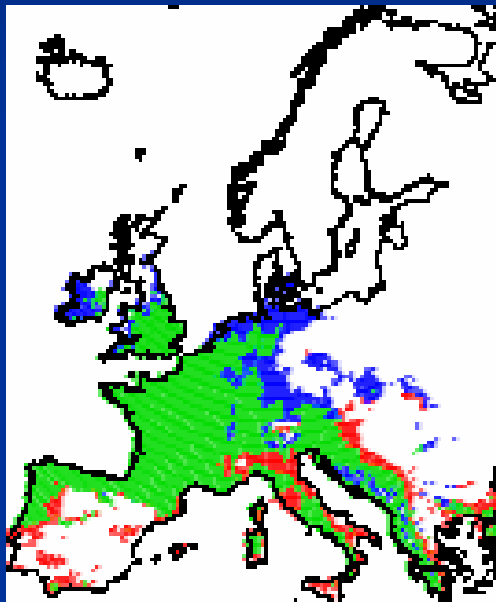
Theory and experimental evidence suggest that small populations have reduced fitness because of increased inbreeding depression, drift load and reduced mate availability. Genetic rescue may come from outbreeding gene flow.

Willi & Fischer (Heredity) 2005

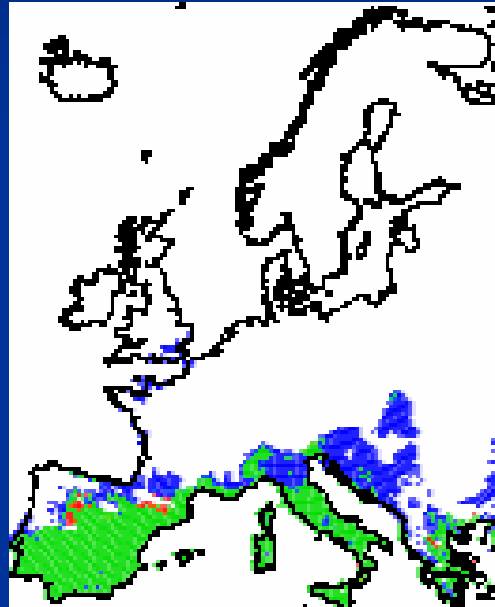
Most European taxa have congeners or rear edge populations in the Mediterranean, which hold higher genetic diversity than they do. If their census size is sufficient, they should be locally adapted.

Not all species are predicted to undergo extirpation under global climate change (climate envelope models) and ranges will be modified making congeneric contact zones likely

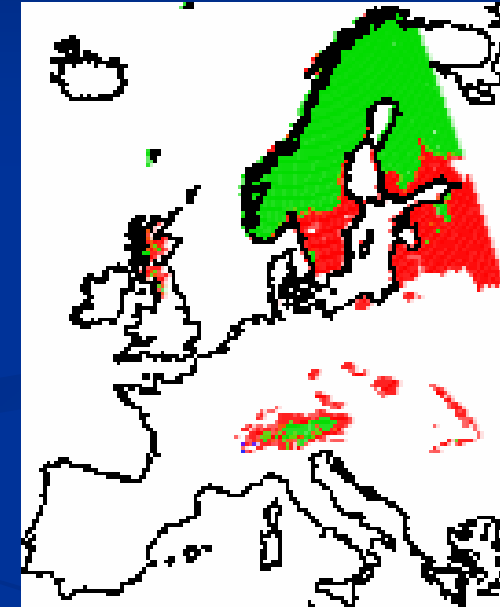
Castanea sativa



Pinus halepensis



Betula nana



Comparison of current and projected (2050) distributions of *C. sativa*, *P. halepensis* and *B. nana*: **Green = favorable habitat now and in 2050**, **blue = favorable habitat in 2050 (but not now)**, **red = favorable habitat now but not in 2050**. (Thuiller 2003)

The trailing edge: genetic implications

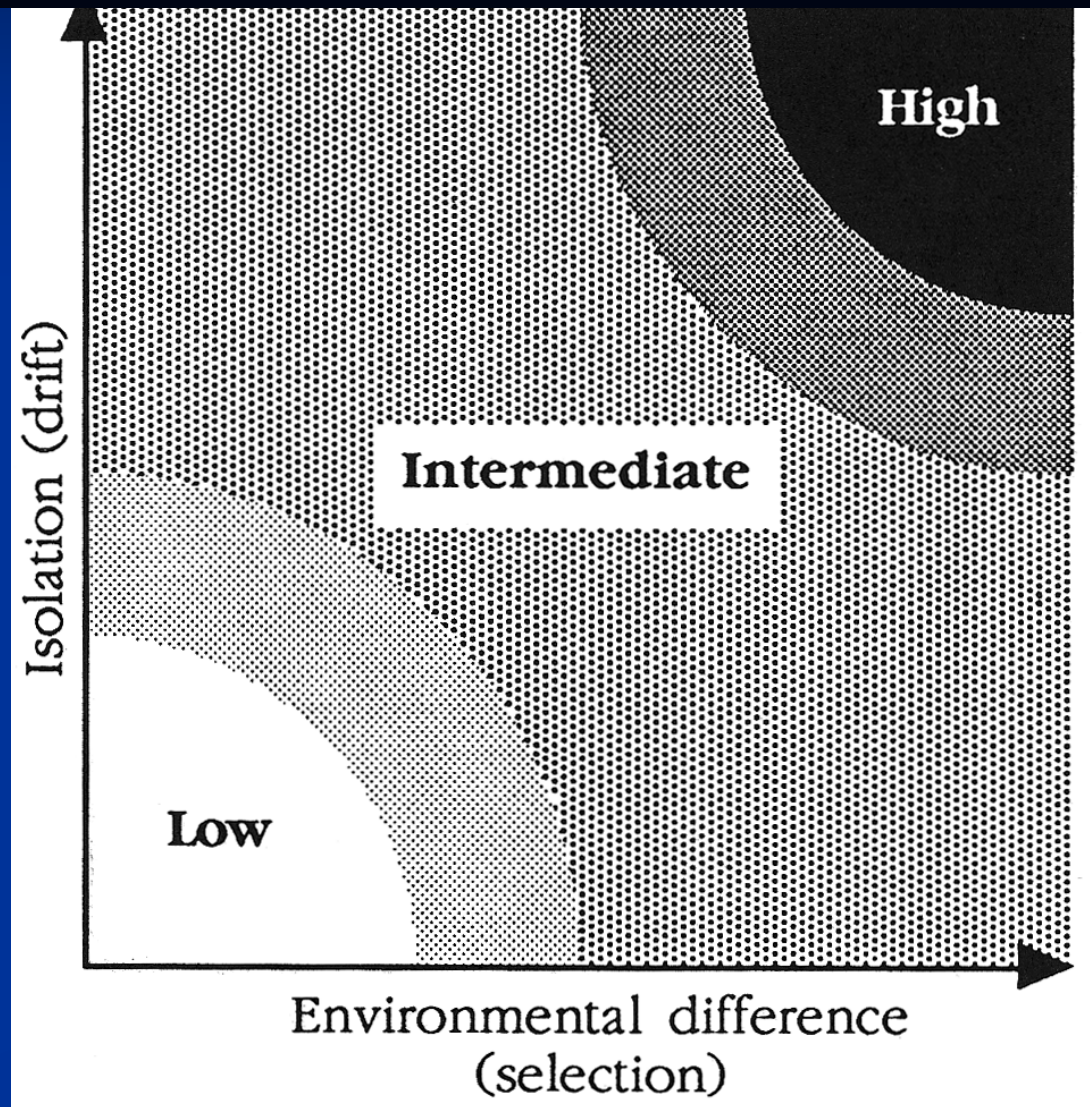
Marginal (trailing edge) populations are less diverse and less adapted than core populations. However, there are as many genetic consequences of being at the receding edge than there are species and past evolutionary trajectories.

The (eastern) Mediterranean, a reservoir of genetic diversity when species ranges change.

Current evidence on genetic consequences of being at the rear edge derives from case studies not initially designed to test that. A general framework for the genetic effect of being at the rear edge, based on solid evidence and theory, is needed. It should include demographic and genetic perspectives.

The trailing edge: genetic implications

Expanding the conservation biology approach of Lesica and Allendorf (1995). When do marginal populations hold an evolutionary interest?



The trailing edge: genetic implications

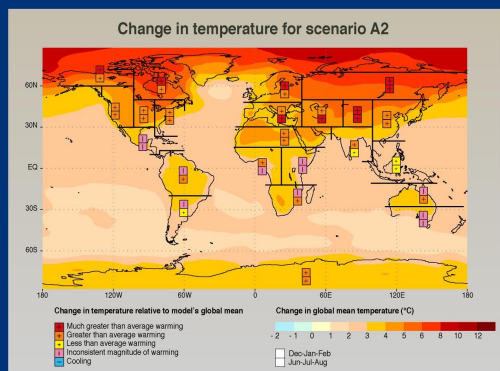
Expanding demographic approaches of range margins to a combined evolutionary – demographic (demo-genetic) approach?

“How influences on the different terms of the equation $N_{t+1} = N_t + i + b - d - e$ can determine range limits, where N is population size; t is time; i is the number of immigrants; b is the number of births; d is the number of deaths; and e is the number of emigrants”
(*Gaston 2009*).

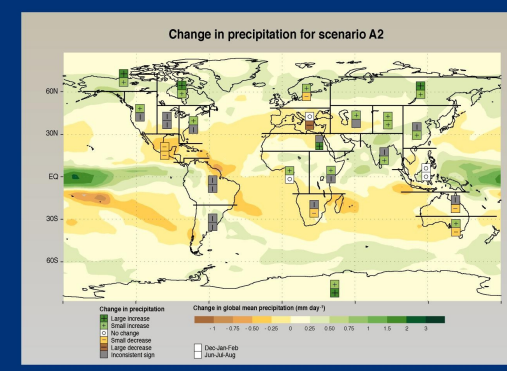
Evoltree SEA workshop - Sopron, Hungary, 11-14 May 2009

The trailing edge: genetic implications
A need for a general demo-genetic framework on the genetic consequences of what it means to be at the trailing edge

Thank you for your attention !



SYR - FIGURE 3-2 a



SYR - FIGURE 3-3 a