Ecological and phylogenetic limits to adaptation in forest sedges

Single-nucleotide deletion causing a change in the product

Ecological and phylogenetic limits to adaptation in forest edges

Large amount of new material by horizontal transfer

How will plant populations and communities respond to global change?

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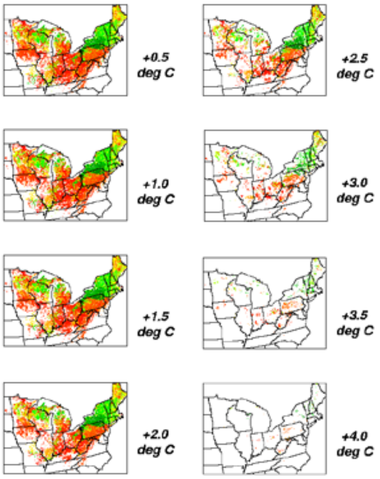
Graham Bell

EVOLTREE San Lorenzo de el Escorial
June 2010

Carex gracillima
Mont St-Hilaire, Quebec
Marcia J. Waterway



What do we need to understand in order to predict the evolutionary effect of environmental change on the distribution and abundance of a species?

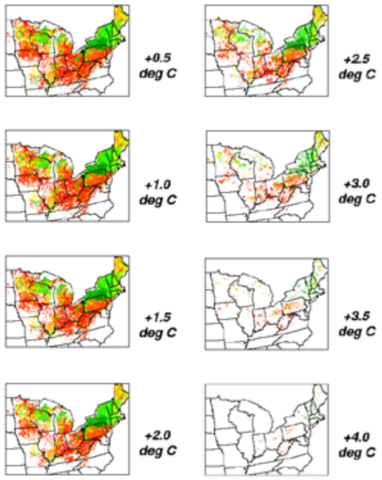
- We need to be able to evaluate the precision of local adaptation in contemporary populations.

- We need to be able to find out whether or not the species is capable of adapting to the change.

- We need to know whether adaptation, if it occurs at all, will rescue the species from extinction.

- We also need to know whether other species are likely to adapt, and if so how this will affect their interaction with the focal species.

- We need to know how the range of the species is likely to change, given that it is able to persist.



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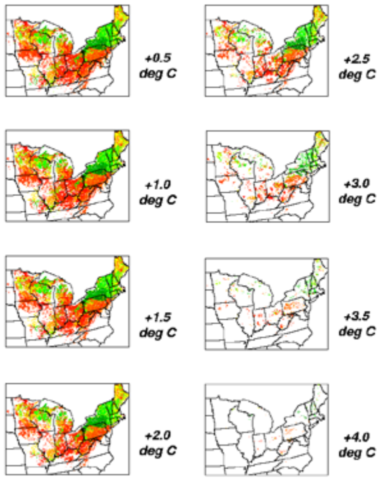

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What can be done?

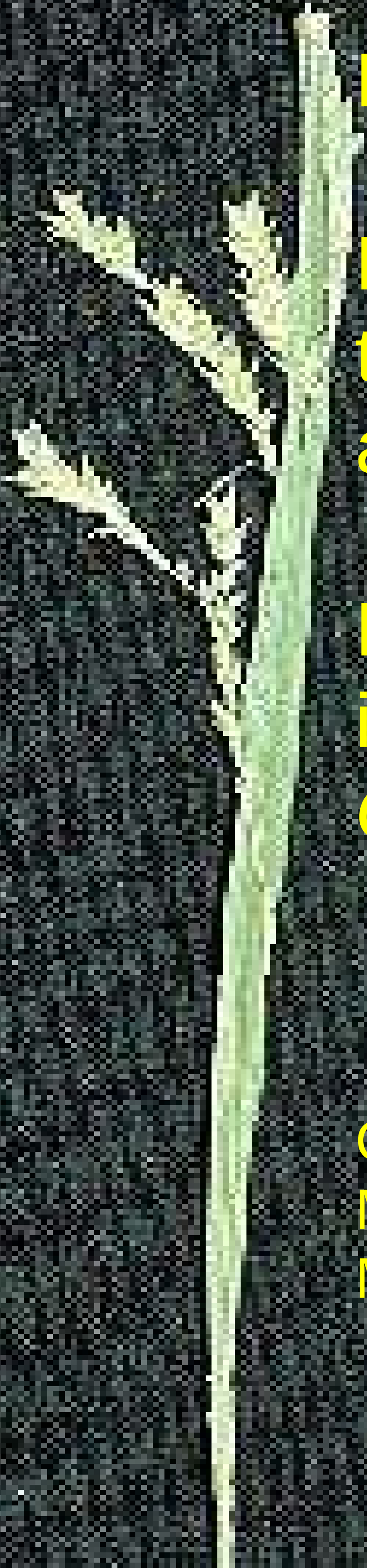
What can we learn about the effects of global change on species and communities through studies of more tractable organisms?

1. Eco-regional trends in adaptation
- ❖ *Local adaptation in forest sedges*

2. Evolutionary responses under climate change
- ❖ *Adaptation to elevated* CO_2 *by algae*

3. Community responses under climate change
- ❖ *Long-term response of phytoplankton communities to elevated* CO_2

4. Evolutionary rescue: adaptation in a deteriorating environment.
- ❖ *The U-shaped rescue curve*
- ❖ *Factors governing rescue*
- ❖ *Model landscapes: local adaptation at forest edges*



Part 1

Eco-regional trends in adaptation

Local adaptation in forest sedges *Carex*

Graham Bell
Marcia J. Waterway
Martin J. Lechowicz

McGill

Marcia J. Waterway (Macdonald College, McGill University) (Director, McGill Herbarium):
Carex phylogenetics

Martin J. Lechowicz (Biology Department, McGill University) (Director, Gault Nature Reserve):
Plant physiological ecology

Species Richness at a Locality: Mont St. Hilaire, Quebec

Great Lakes-St. Lawrence Forest

...old-growth with trees to 450+ year

Outer slopes ↑

MONT ST-HILAIRE

Interior basin ↓

Carex (sedges)

About 2000 species worldwide

About 60 species at Mont St-Hilaire (1000 ha)

Carex plantaginea

Carex prasina

Mont St-Hilaire sedges

Carex communis

Carex pedunculata

Carex rosea

Carex appalachica

Carex scabrata

Carex gracillima

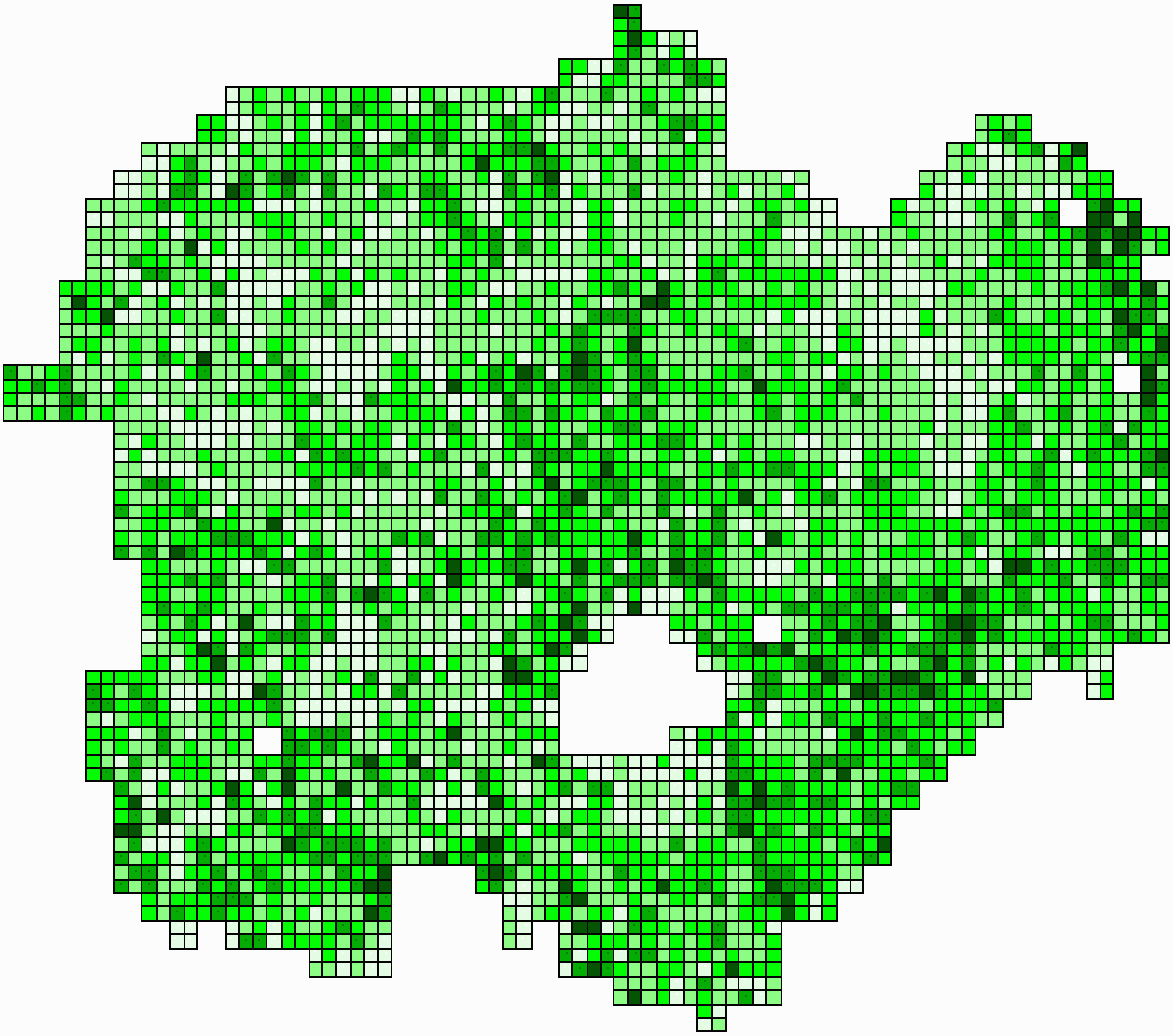
Carex pensylvanica

Carex albursina

Carex deweyana

Carex leptalea

The biological survey:
Carex species diversity at Mont St-Hilaire

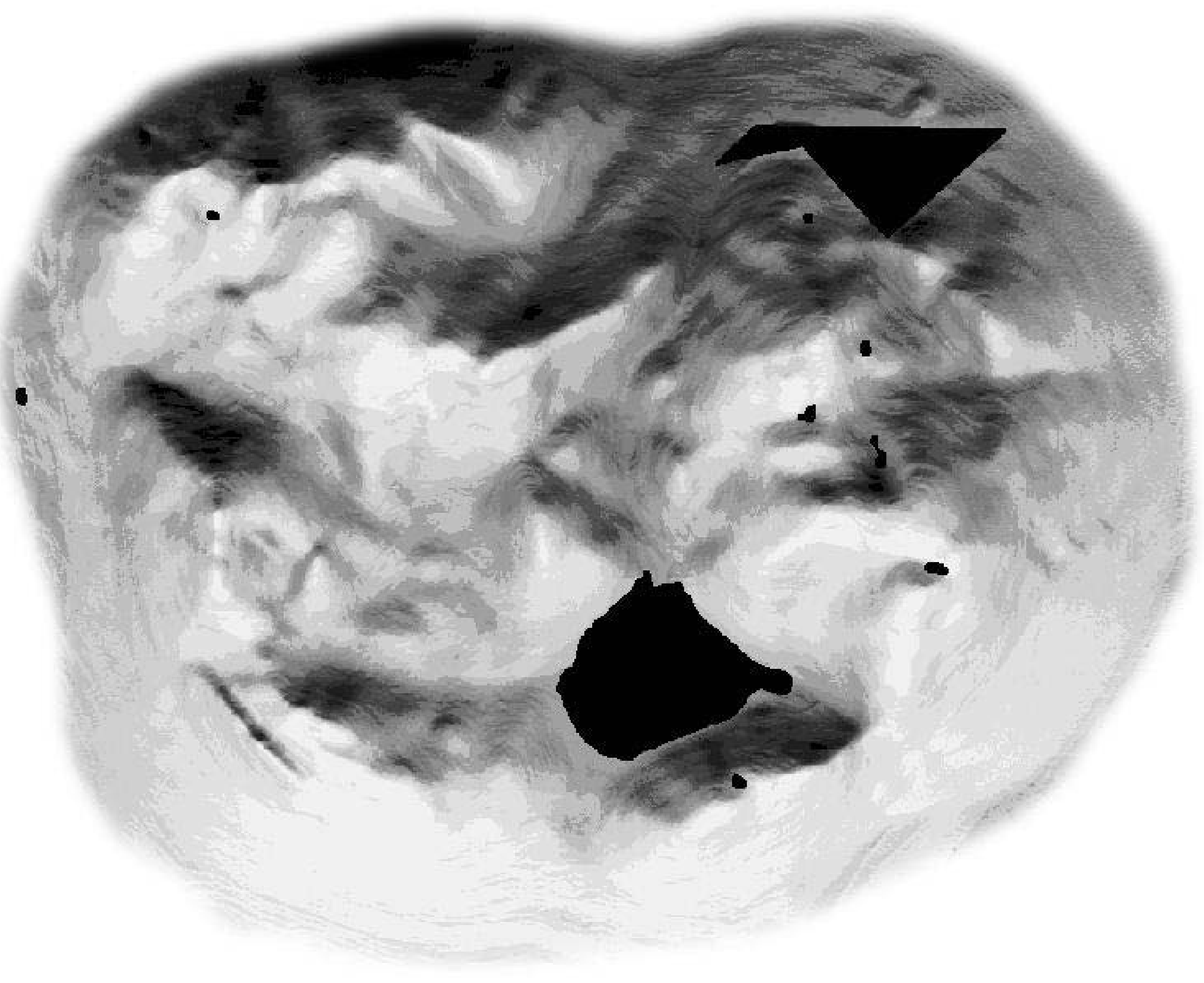


The grid survey. Grain: 0.25 ha. Extent: 1016 ha
The transect survey. Grain: 2m. Extent: 27000m

Total data available: about 2 x 10^6 spatially located records.

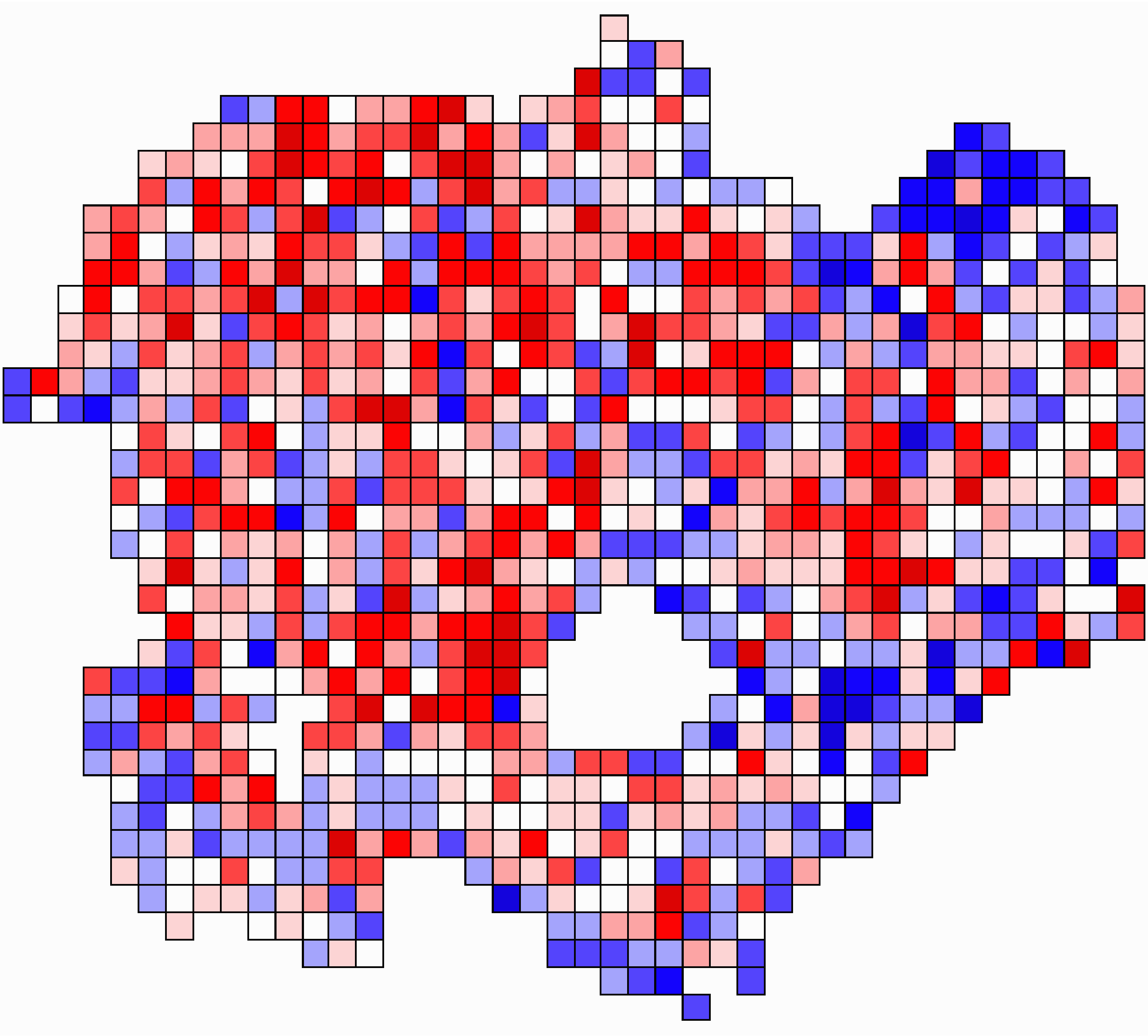
The environmental survey
DEM: insolation

Grain: 5x5m

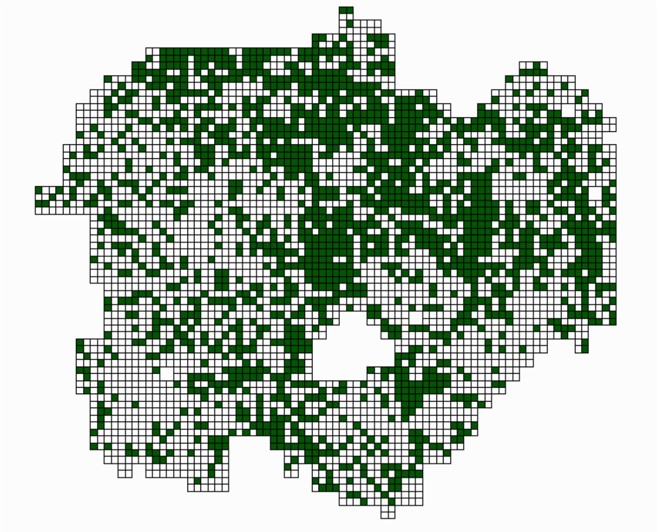


The environmental survey
Soil pH

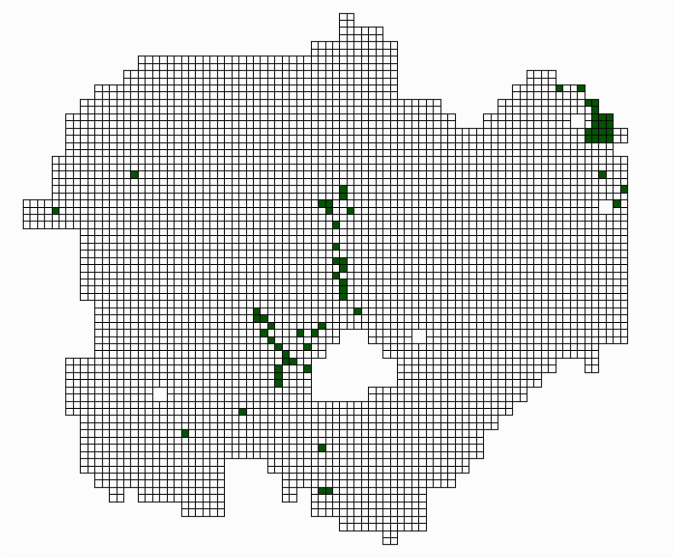
Grain: 1 ha



The co-distribution of species reflects the degree of joint specialization



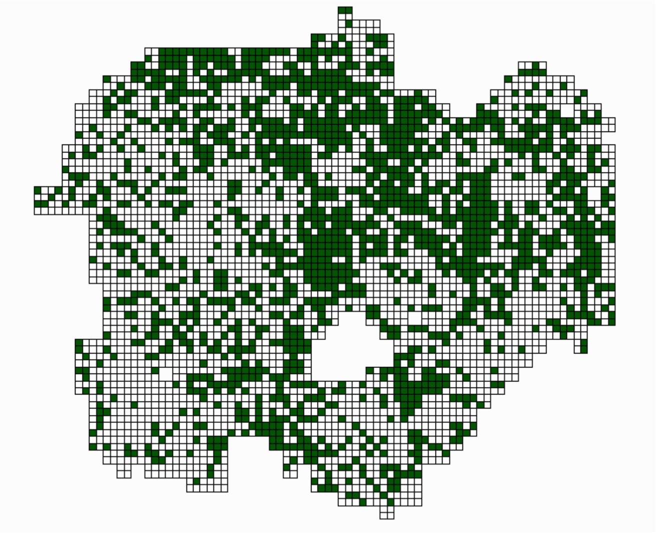
Carex arctata



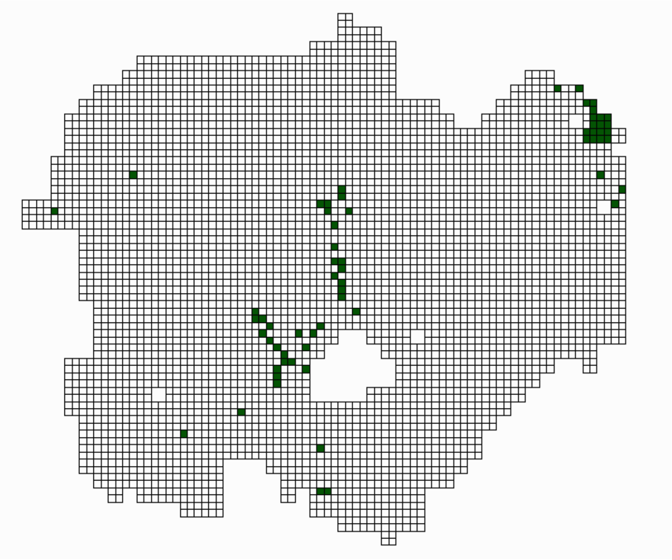
Carex prasina

Environmental correlates and co-distribution will enable us to estimate the precision of local adaptation provided that the biological survey is sufficiently detailed and extensive.

The co-distribution of species reflects the degree of joint specialization



Carex arctata

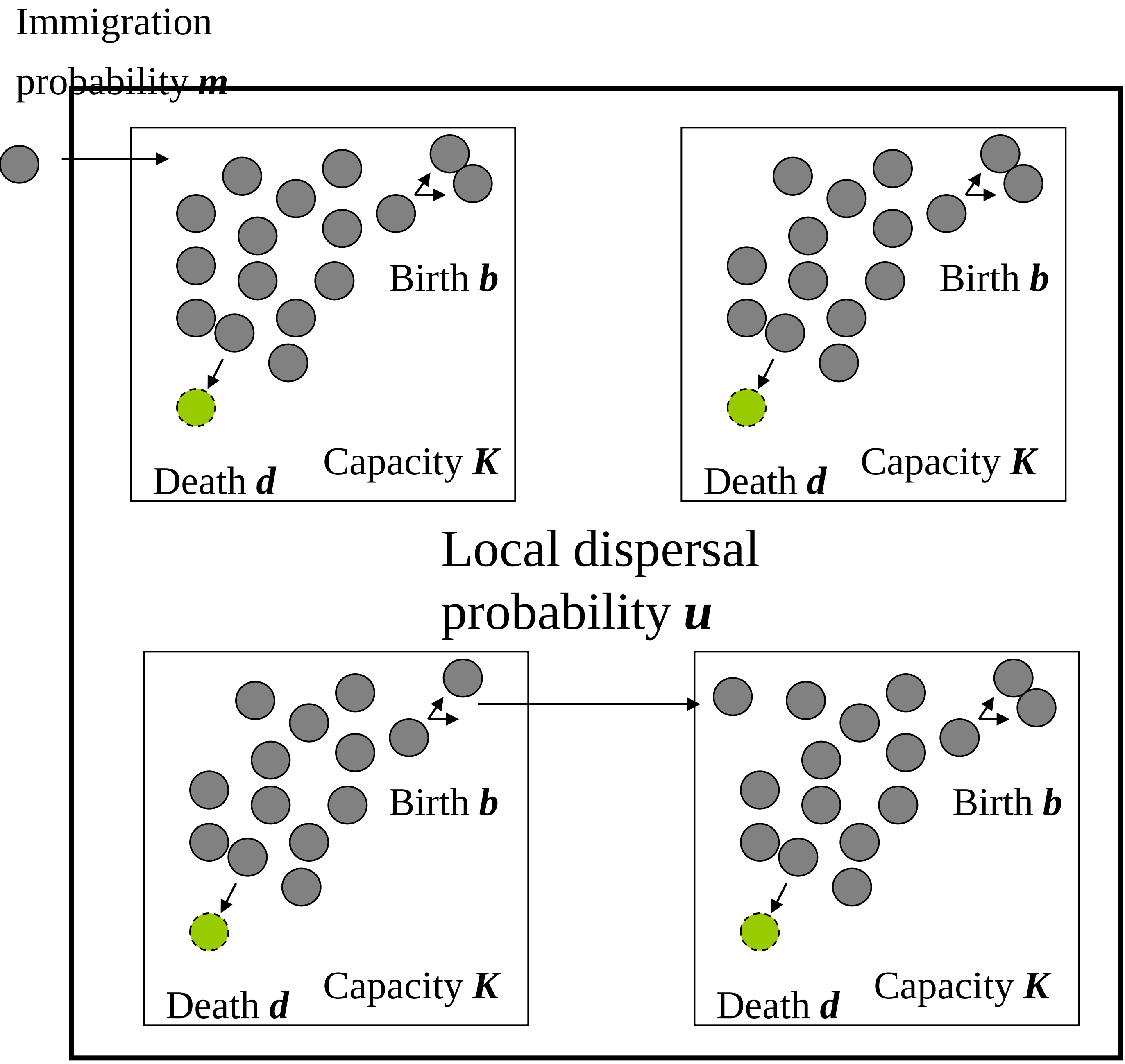


Carex prasina

Environmental correlates and co-distribution will enable us to estimate the precision of local adaptation provided that the biological survey is sufficiently detailed and extensive.

Unfortunately, this statement is erroneous.

The spatially explicit neutral community model



Immigration probability ***m***

Birth ***b***

Death ***d***

Capacity ***K***

Birth ***b***

Death ***d***

Capacity ***K***

Local dispersal probability ***u***

Birth ***b***

Death ***d***

Capacity ***K***

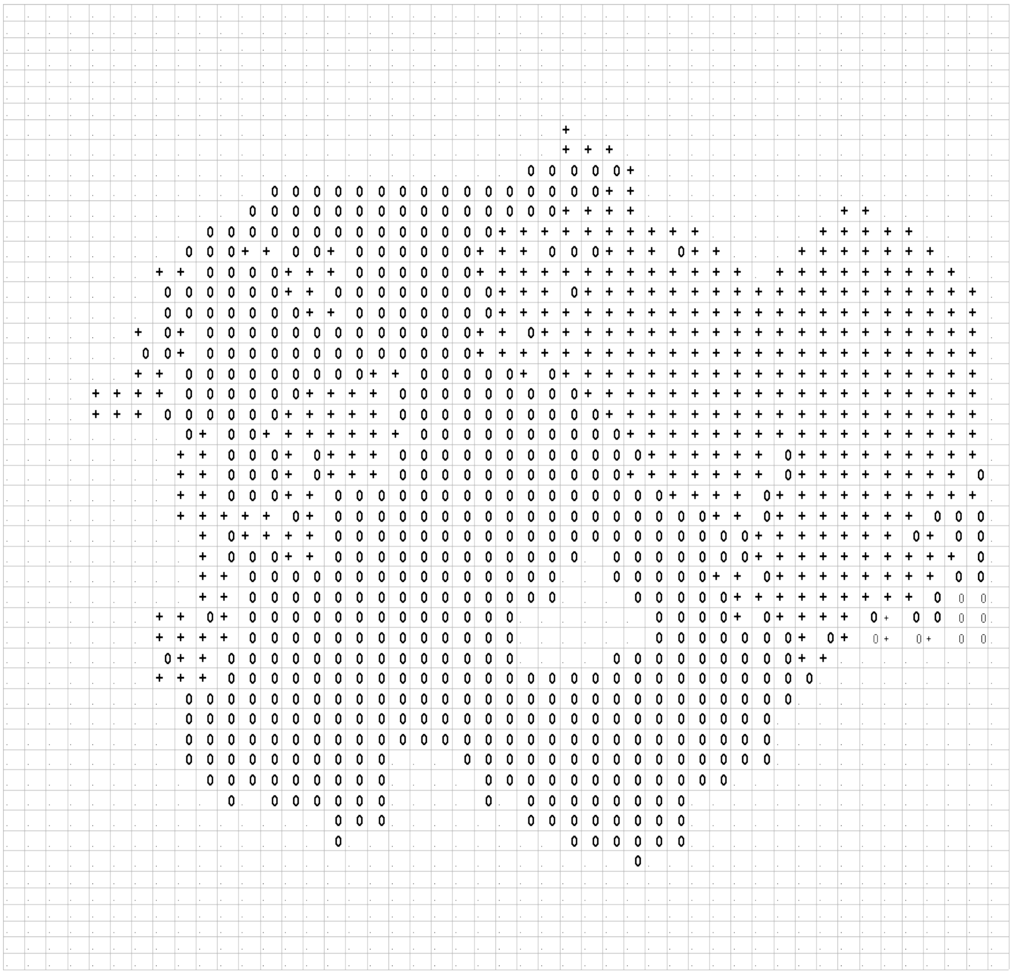
Birth ***b***

Death ***d***

Capacity ***K***

This simple model generates all the familiar macro-ecological patterns such as the distribution of abundance, species-area relationship, range-abundance relationship, turnover etc.

A surprise: neutral community model output often resembles the patterns shown by species in biological surveys.



Consequently, naïve interpretation of survey data is likely to be misleading. It must be reinforced by a more sophisticated treatment of spatial and phylogenetic scale.

The problem of spatial scale

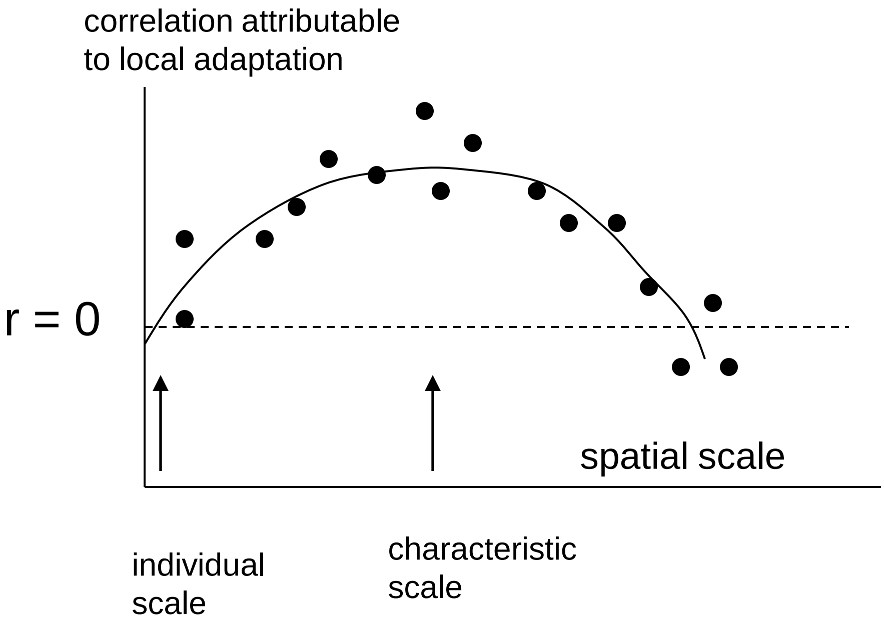
Given that a species is specifically adapted to a range of conditions which vary in space at some characteristic scale.

Grain < characteristic scale: weak signal because most variation among quadrats is intraspecific.

Grain = characteristic scale: strong signal.

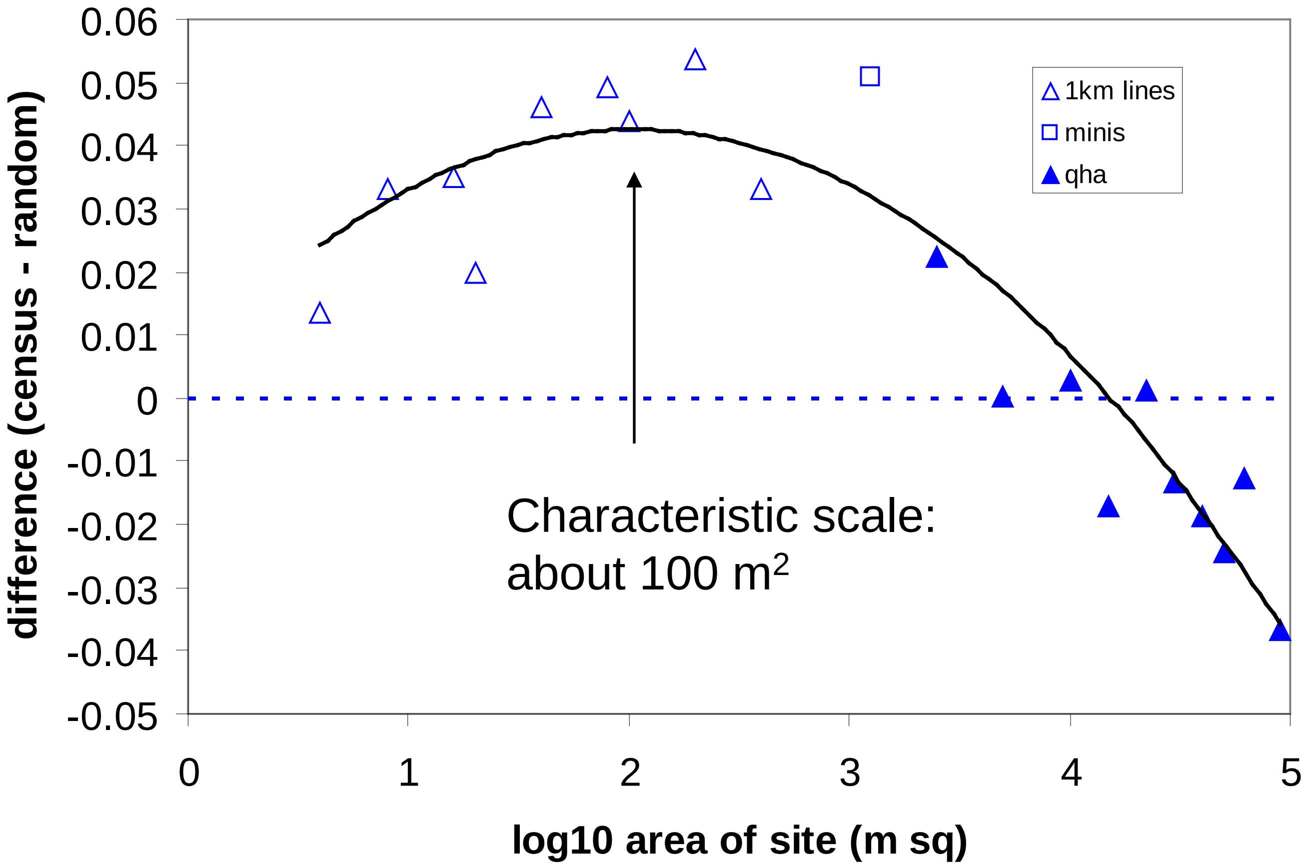
Grain > characteristic scale: weak signal because several species with different adaptation occur within the same quadrat.

(This is necessary but not sufficient to estimate the precision of local adaptation.)



The co-distribution of similarly adapted species is maximized at an intermediate spatial scale

Carex sister species co-distribution over 5 orders of magnitude at Mont St-Hilaire



Characteristic scale:
about 100 m^2

Bell, Waterway & Lechowicz (unpublished)

The problem of phylogenetic scale

Given that lineages acquire specific adaptation at a characteristic phylogenetic level through the intermittent fixation of beneficial mutations.

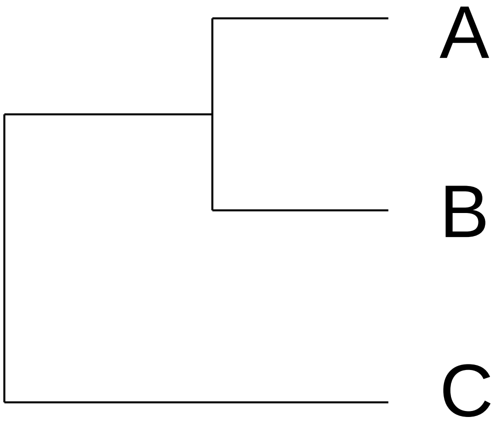
Taxa < characteristic level: weak signal because closely related lineages are nearly neutral.

Taxa = characteristic level: strong signal.

Taxa > phylogenetic level: weak signal because each taxon includes divergently adapted lineages.

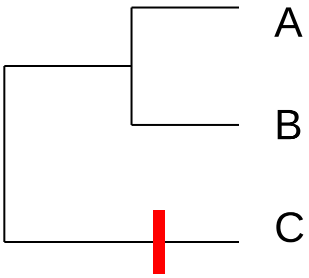
(This is sufficient to demonstrate local adaptation provided that speciation has not taken place *in situ*.)

Sister-group analysis

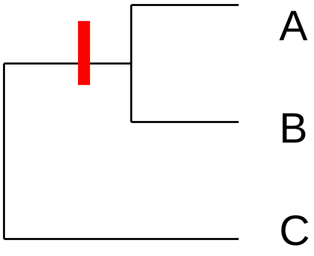


Sister species in set included in biological survey

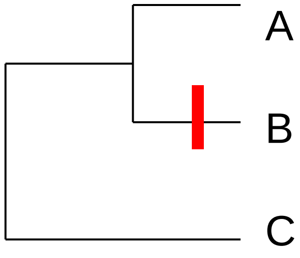
Most closely related outgroup in survey



Speciation occurs independently of innovation in outgroup: sister species are more similar to each other than they are to outgroup.

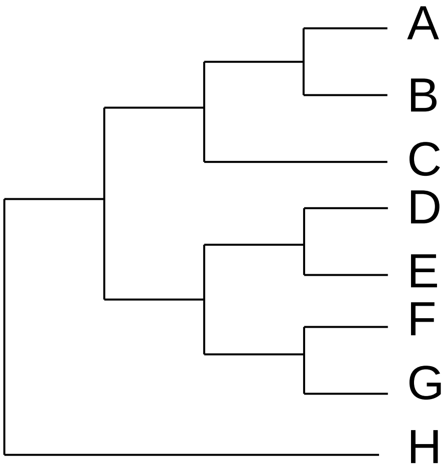


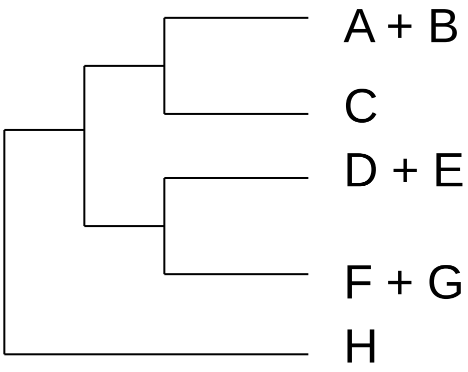
Speciation occurs independently of innovation in common ancestor: sister species are again more similar to each other.

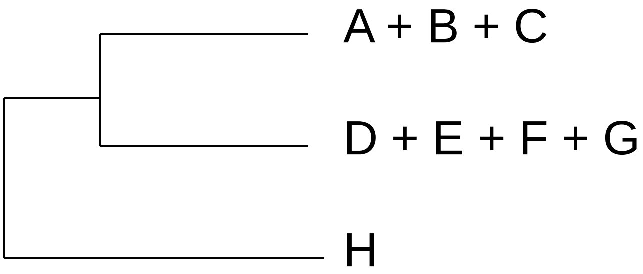


Speciation associated with innovation in one of sister species in outgroup: sister species are less similar to each other than they are on average to outgroup.

Sister species can be combined into successively more inclusive clades, repeating the analysis at each level.



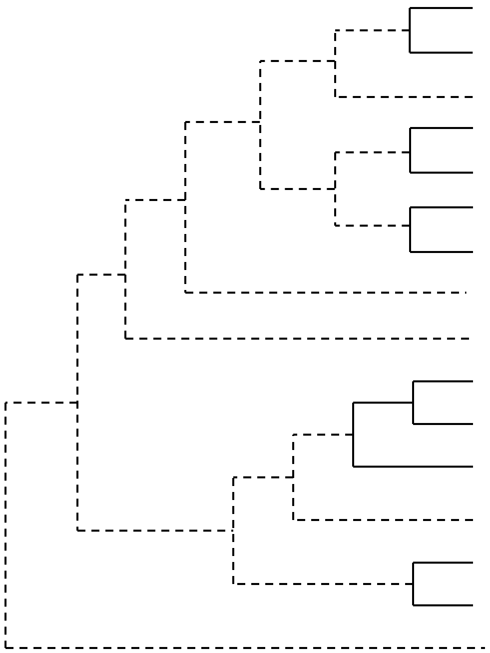




(no outgroup)

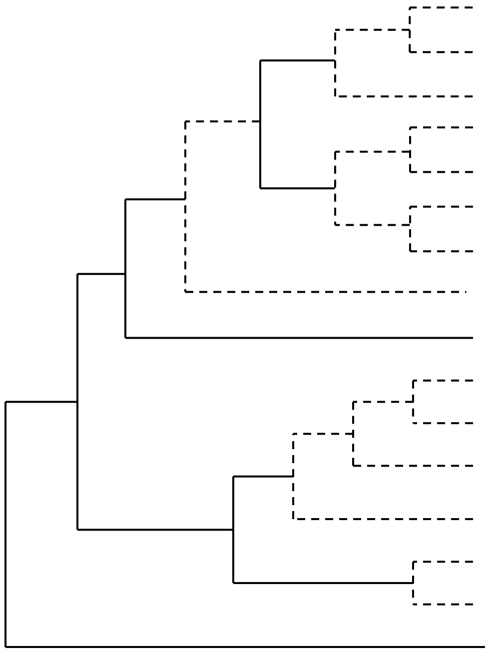
The level at which co-occurrence is observed reflects the level at which the neutral interpretation fails.

Criterion (solid lines): $r_{AB} > r_{AB.C}$
and r_{AB} > randomized data.



Sister species are similar. The neutral theory fails completely.

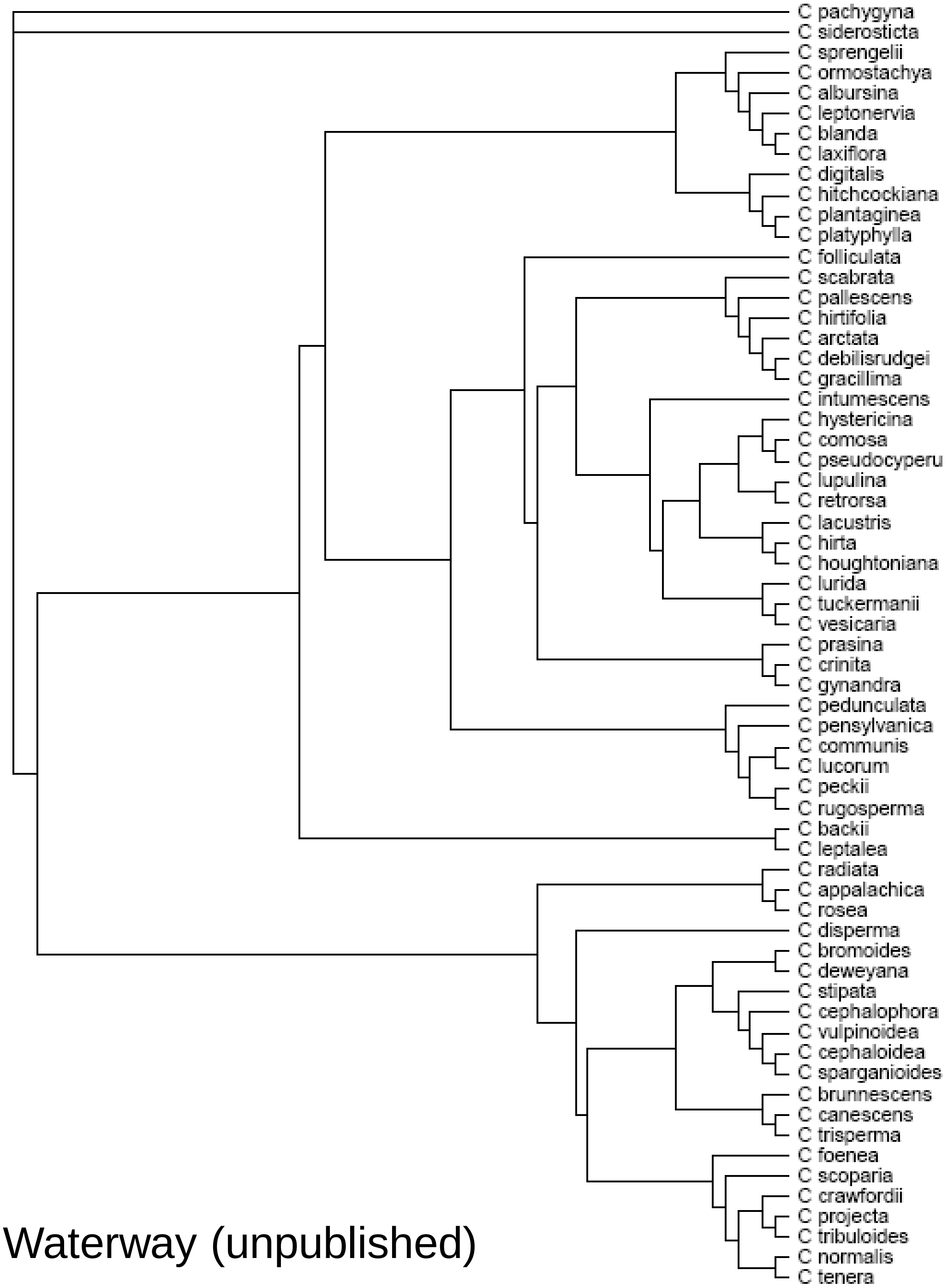
The neutral theory also fails if sister species are consistently dissimilar.



Similarity is expressed at higher levels. The neutral theory may hold at lower levels.

Mont St-Hilaire clip of *Carex* phylogenetic tree

MSH parsimony tree, 63 taxa
2 nuclear genes (ETS, ITS)
5 chloroplast genes (matK,
rps16, rpl16, trnL-F, trnE-Y-D)

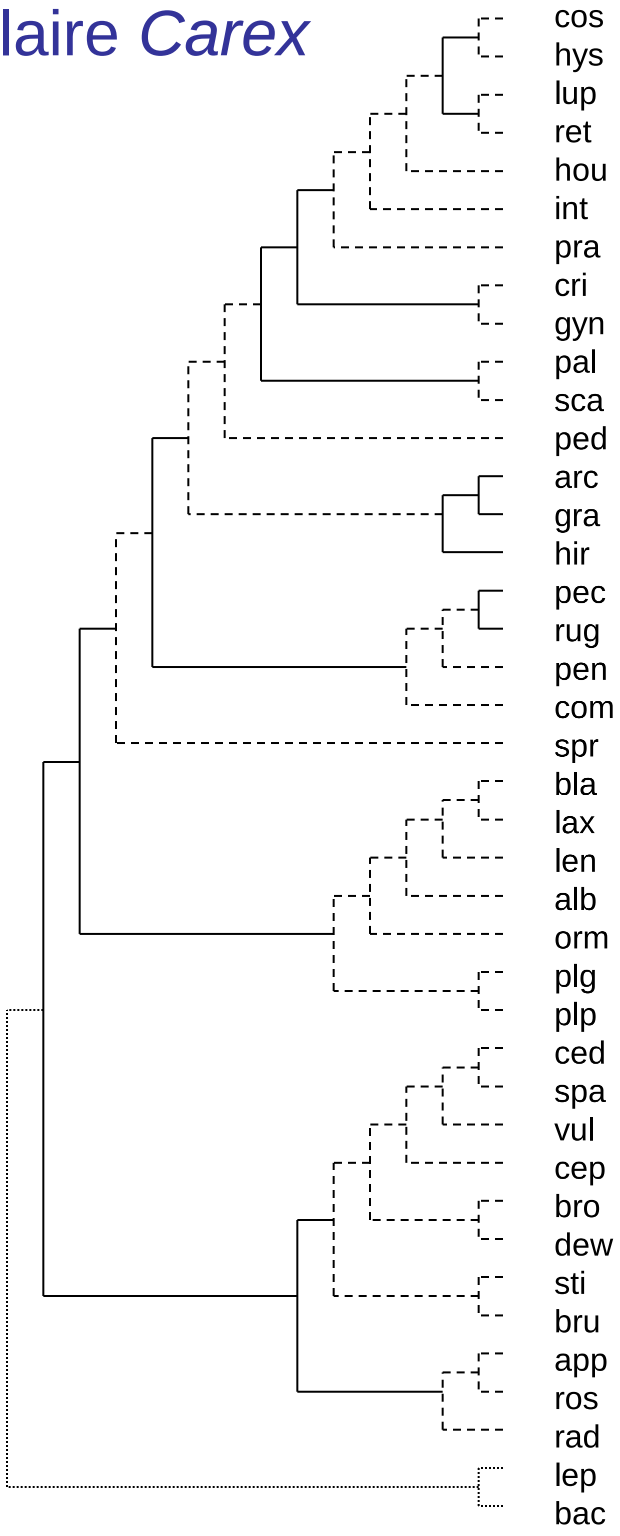


M.J. Waterway (unpublished)

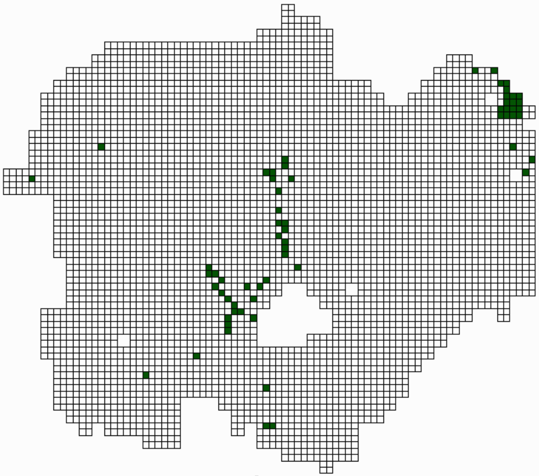
Sister-group comparisons for the Mont St-Hilaire *Carex*

Criterion:

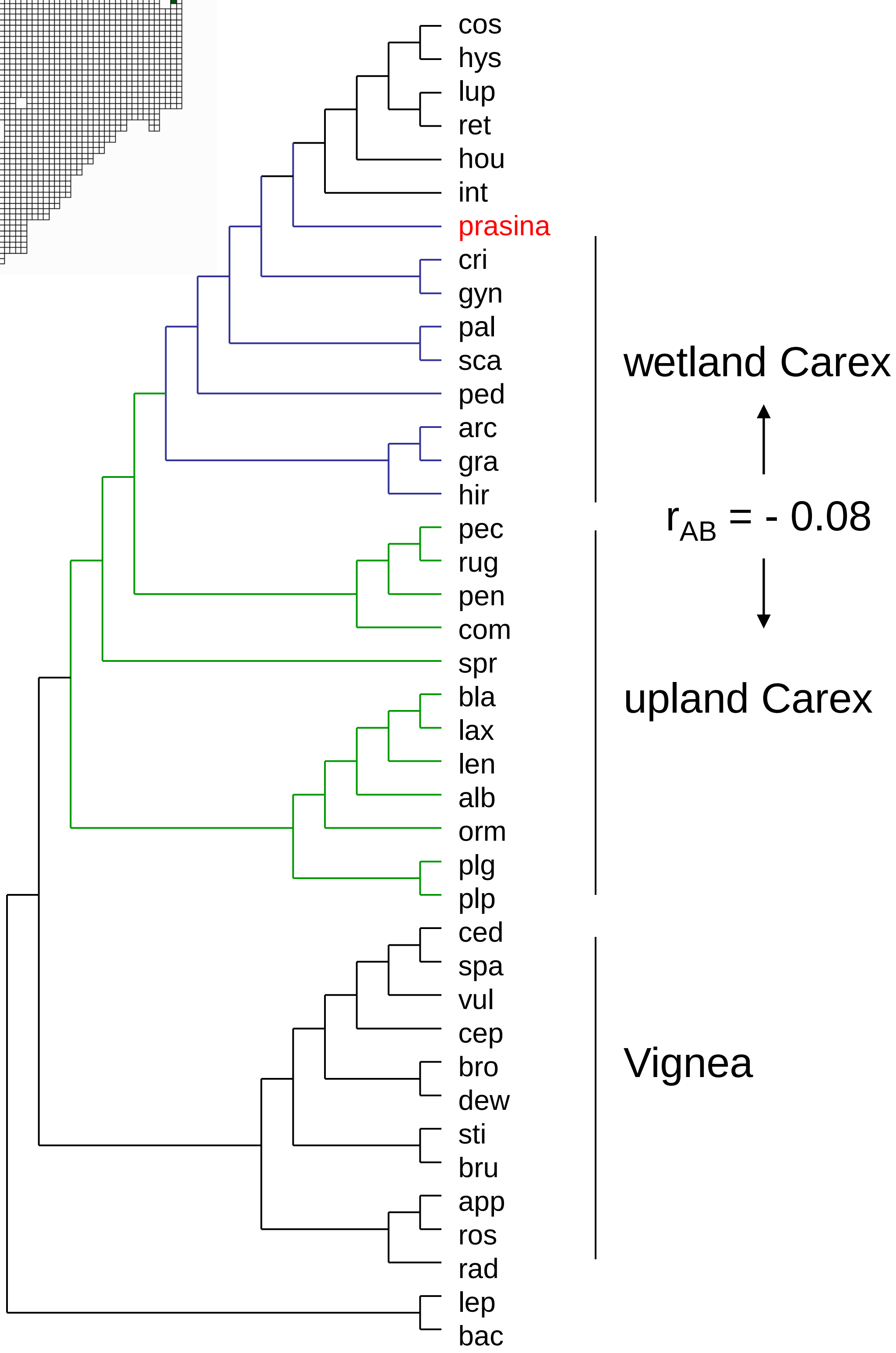
$r_{AB} > 0.1$ and $r_{AB} > r_{AB.C}$



Bell, Waterway & Lechowicz (unpublished)



Carex prasina



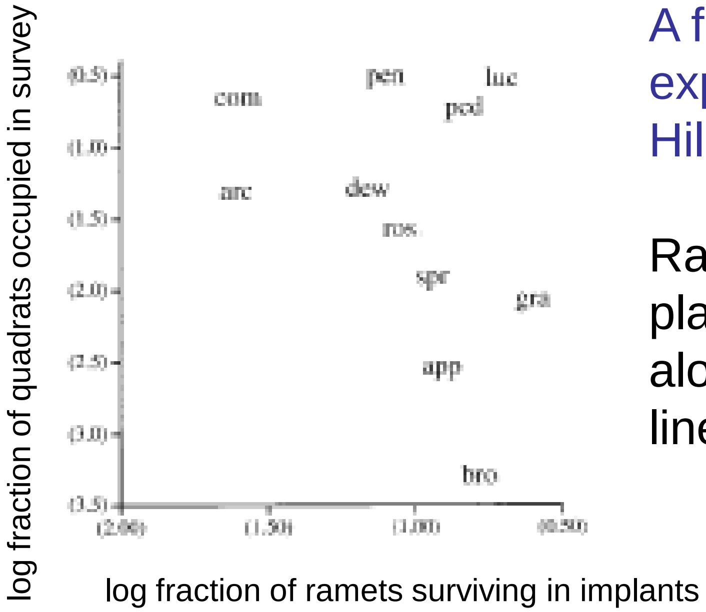
$r_{AB} = - 0.08$

Bell, Waterway & Lechowicz (unpublished)

The inevitability of experimentation

The interpretation of surveys is always tentative because stochastic effects are large relative to directional effects caused by natural selection. Experiments are the only secure source of understanding.

FIELD EXPERIMENTS are ideal but are very laborious and are vulnerable to stochastic processes.



A field implant experiment at Mont St-Hilaire

Ramets of 14 species planted at 10m intervals along 3 1km survey lines (= 4200 implants).

LABORATORY EXPERIMENTS are therefore necessary although they lead to difficult problems of extrapolation from the microcosm to the field.

Physiological processes that respond to selection.
Ecological processes that govern the response to selection.

Part 2: Evolutionary responses to climate change

Experimental evolution of algae at high CO_2

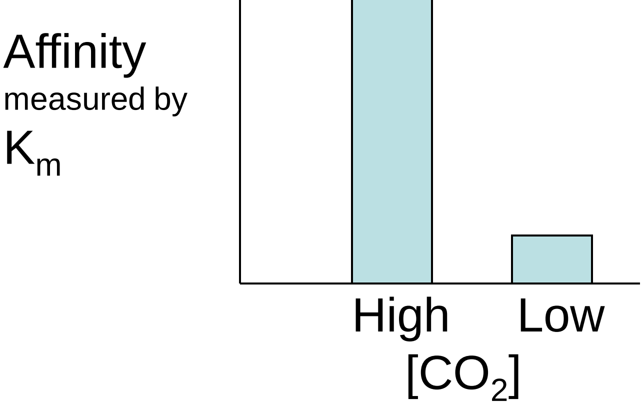
Sinéad Collins (McGill)

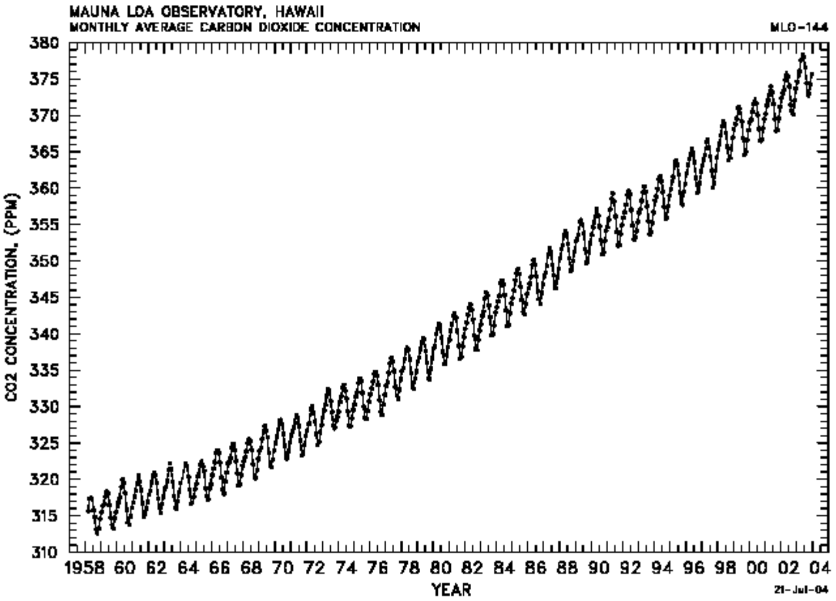
Collaborator: Dieter Sültemeyer (Kaiserslaüten)

Plasticity of photosynthesis

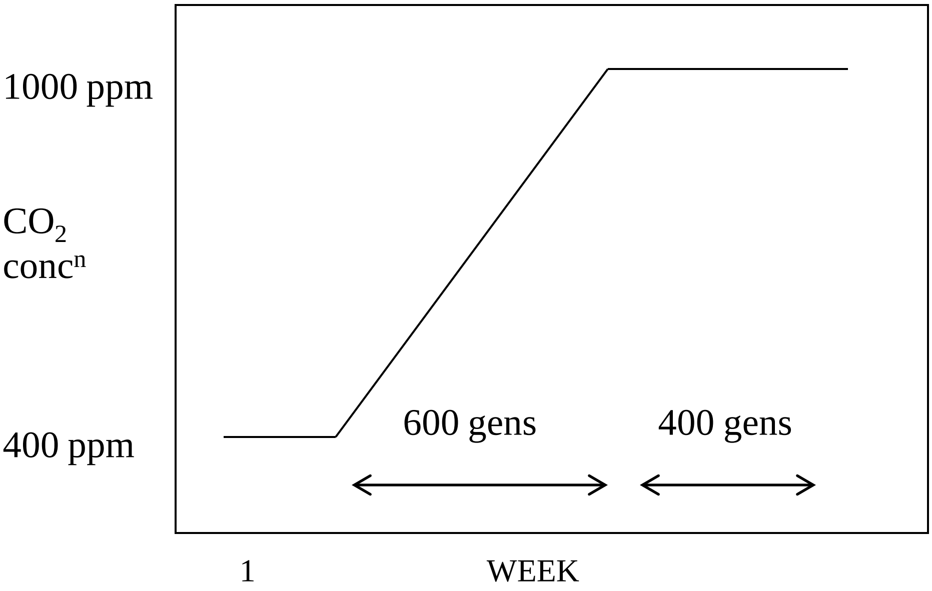
Most eukaryotic algae respond to CO_2 limitation by inducing a carbon-concentrating mechanism (CCM) that increases CO_2 concentration in vicinity of Rubisco.

CCM is downregulated when CO_2 is abundant



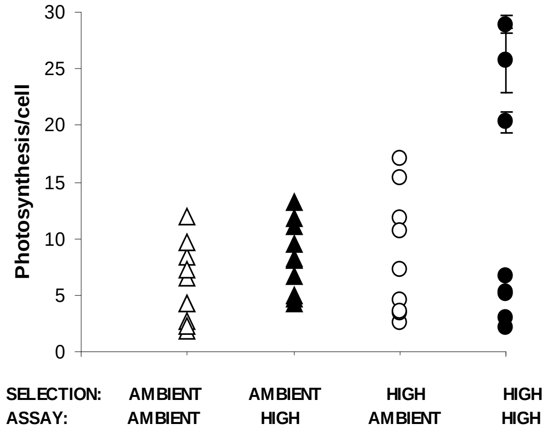


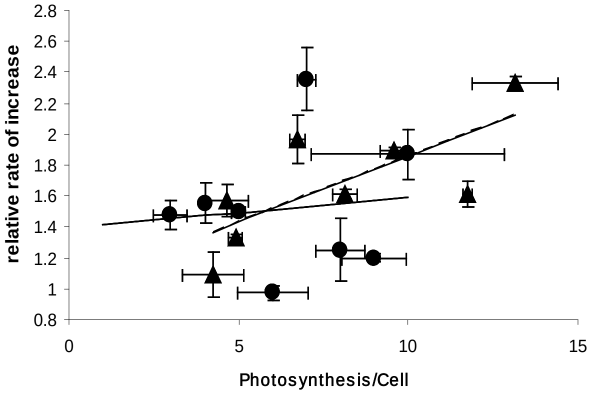
CO_2 is expected to increase from about 400 ppm to about 1000 ppm in the next century



We exposed isogenic lines of the unicellular green alga *Chlamydomonas* to the same rate of increase, scaled to its shorter generation time.

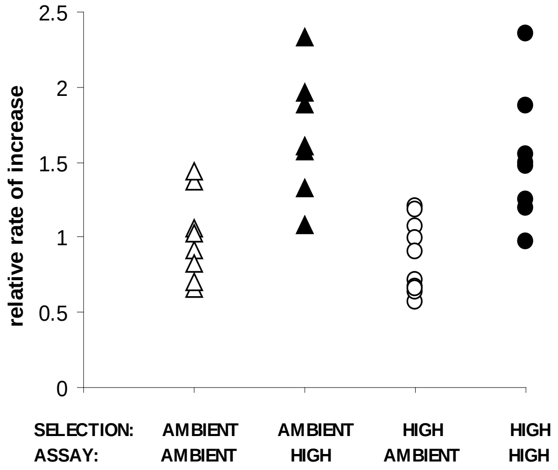
Outcome of 1000 generations of experimental evolution

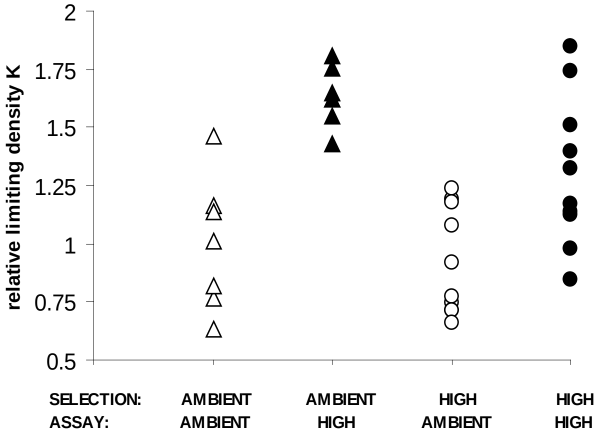




Some (not all) High lines have higher rates of photosynthesis

Photosynthesis is coupled to growth

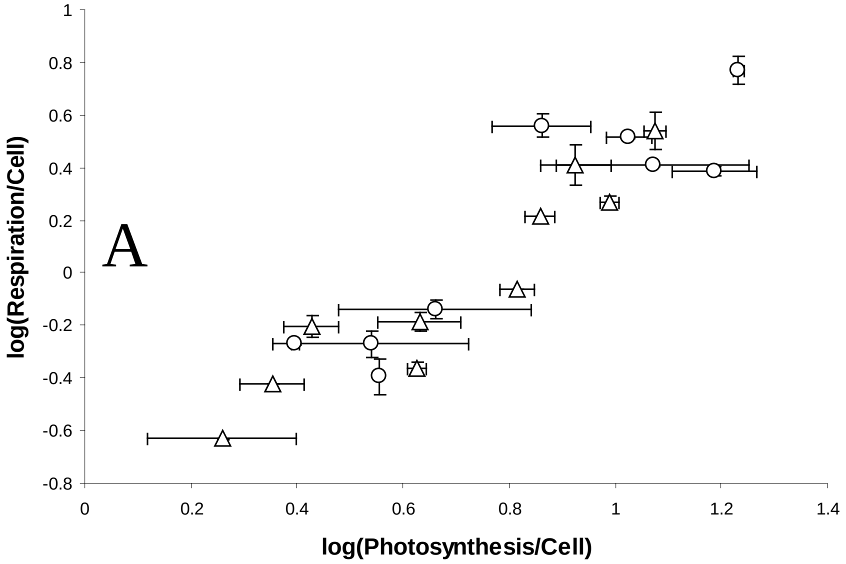




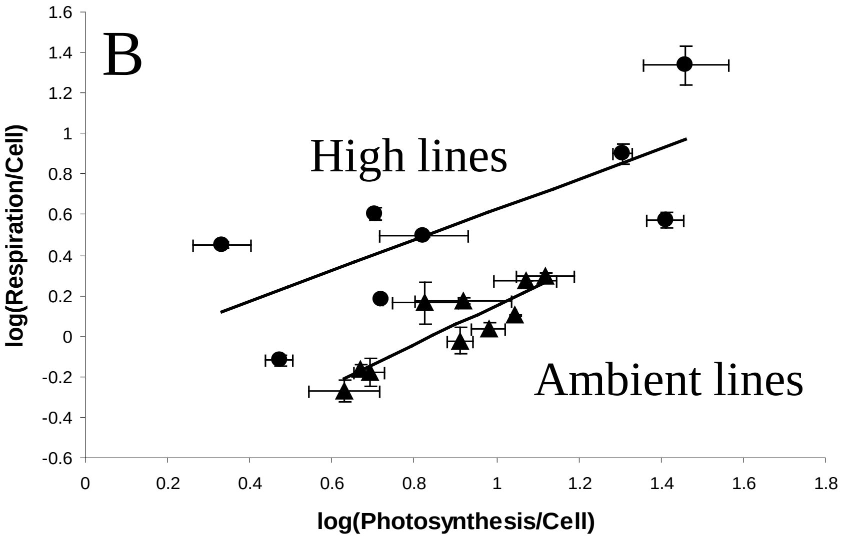
But the High lines do not grow faster at elevated CO_2

Nor do they reach a greater limiting density

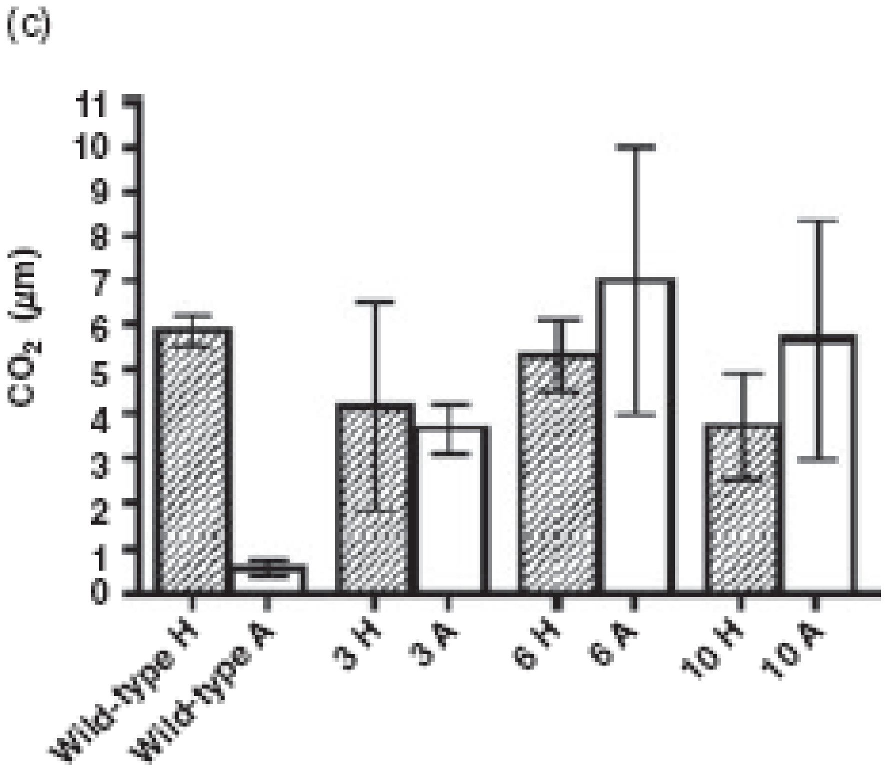
The High lines waste any extra carbon they fix



Photosynthesis and respiration are linked at ambient CO_2



At high CO_2, the High selection lines have greater respiration for given photosynthesis



Regulation of CO_2 uptake

High lines have similar K_m at High CO_2, but are unable to induce high-affinity uptake at low CO_2. The CCM fails to operate properly.

The High-CO_2 phenotype

- Evolution at high CO_2 leads to
  - Degradation of CCM
  - Greater dependence on diffusion
  - Increased leakage of carbon from cell (in some lines)
  - Partly compensated by higher-affinity photosynthesis (in some lines)
- Hence High lines fail to evolve specific adaptation to high-CO_2 conditions.
- When returned to ancestral (ambient) conditions growth may be severely compromised.
- This resembles CCM knock-out phenotypes and may be attributable to accumulation of conditional neutral mutations.

Consequences of the High-CO_2 phenotype

Population net C uptake $U = N V_{net}$

	V_{net}		N (relative)	
	Ambient	High	Ambient	High
Wild type	250.6	371.9	1	1.63
High lines	50.7	286.7	1.12	1.31

U(High)/U(wt) = 0.23 at Ambient CO_2

U(High)/U(wt) = 0.62 at High CO_2

Hence: extrapolating from current physiological parameters leads to a 40% overestimate of net carbon sequestration.

We found similar high-CO_2 phenotypes in soil algae isolated from natural CO_2 springs.

Photo: Bridges et al (www.uni-duesseldorf.de/bridges

This is the Bossoleto CO_2 spring in Italy.

Part 3: Ecological responses to climate change

Long-term response of phytoplankton communities at high CO_2

Etienne Low-Decarie (McGill)
Mark Jewell (McGill)

Collaborator: Gregor Fussmann (McGill)

Preliminary results:

6 species from 3 major clades (cyanobacteria, diatoms, chlorophytes) cultured for 700 generations at rising → elevated CO_2.

There are pronounced shifts in competitive ability that drive changes in community composition at the level of major clades.

Part 4: Evolutionary rescue: adaptation in a deteriorating environment

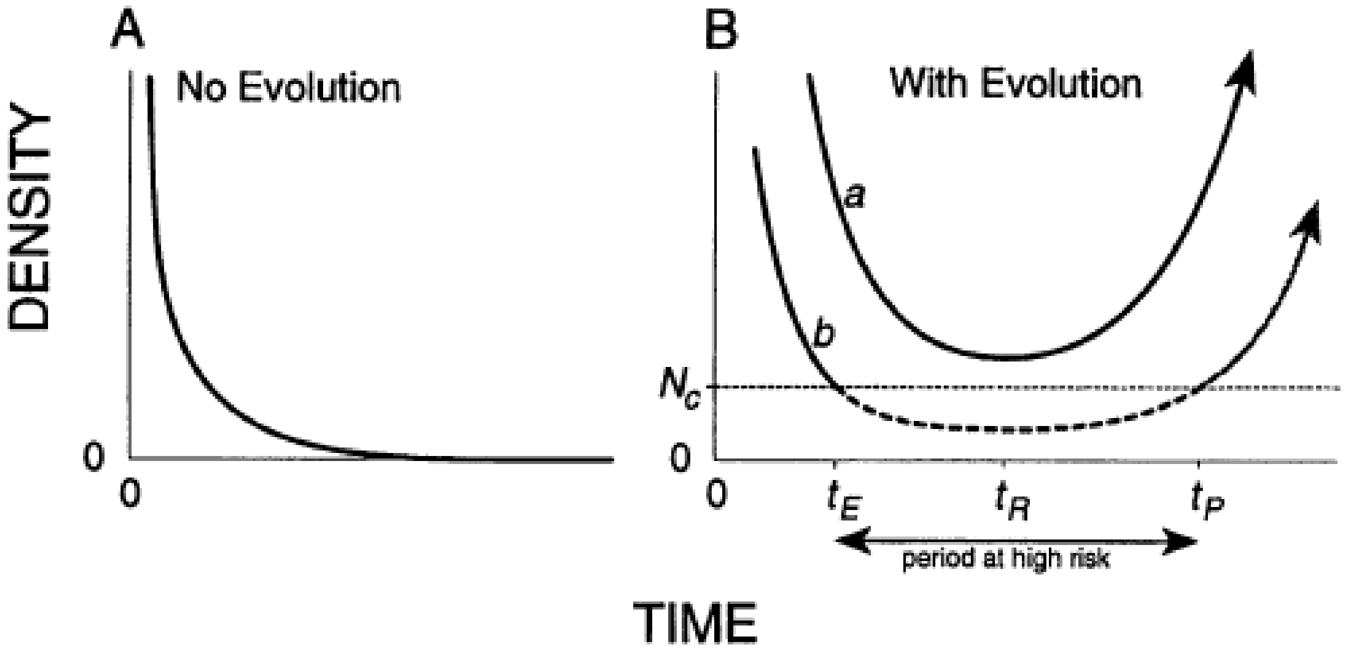
The U-shaped rescue curve.

The factors governing rescue

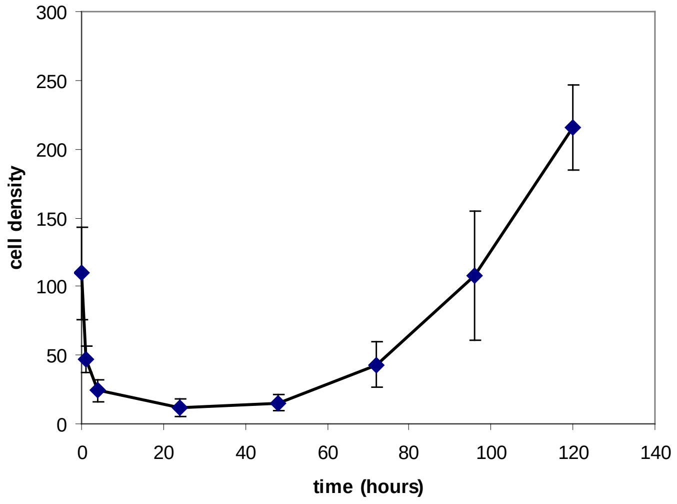
Model landscapes: population structure and the rate of deterioration

Collaborator: Andy Gonzalez

The U-shaped rescue curve



Gomulkiewicz & Holt (1995) Evolution 49, 201

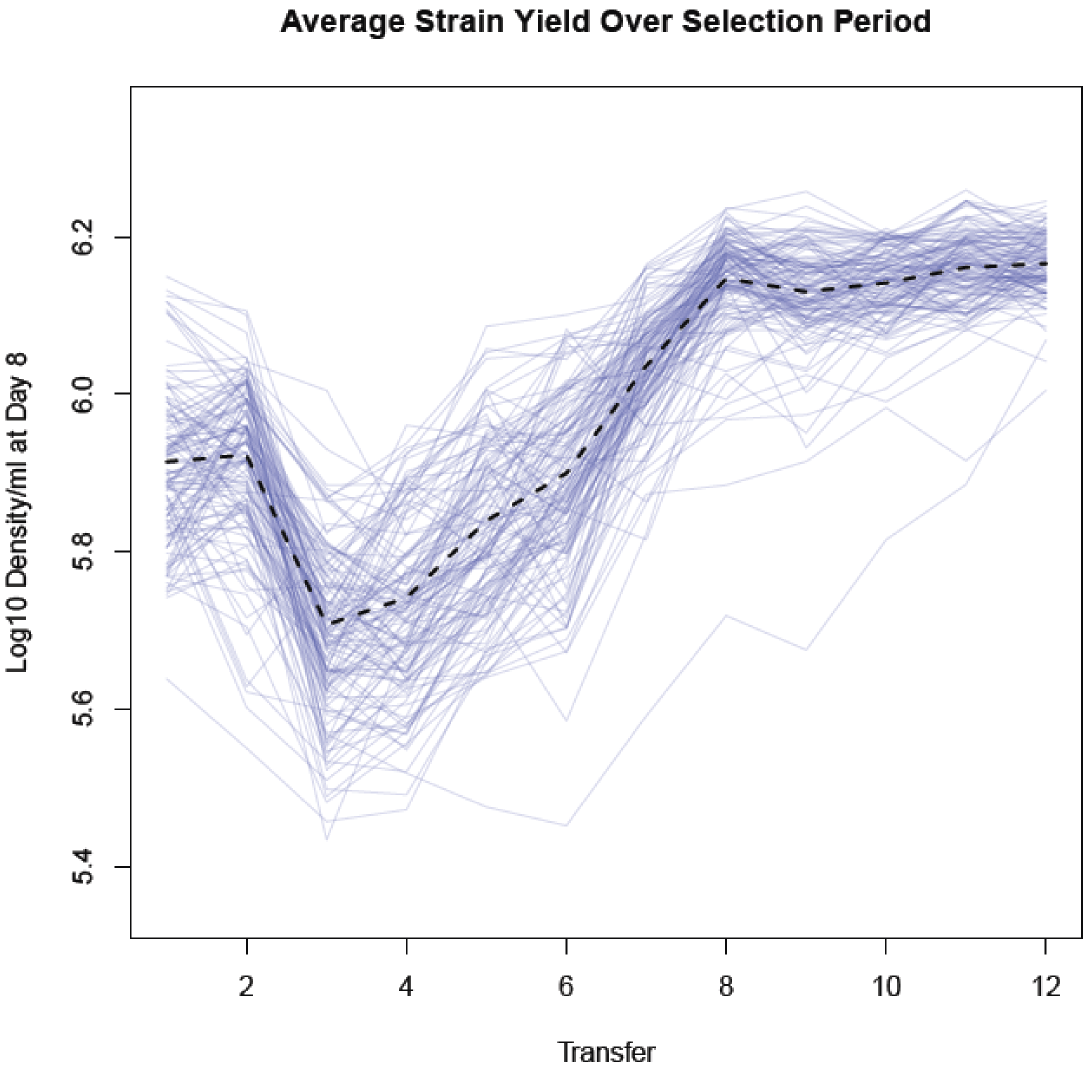


The U-shaped rescue curve documented in the yeast/salt system.

Bell & Gonzalez 2009 Ecol Letters

Evolutionary rescue in experimental cultures of *Chlamydomonas* under salt stress

Chase Moser (McGill)

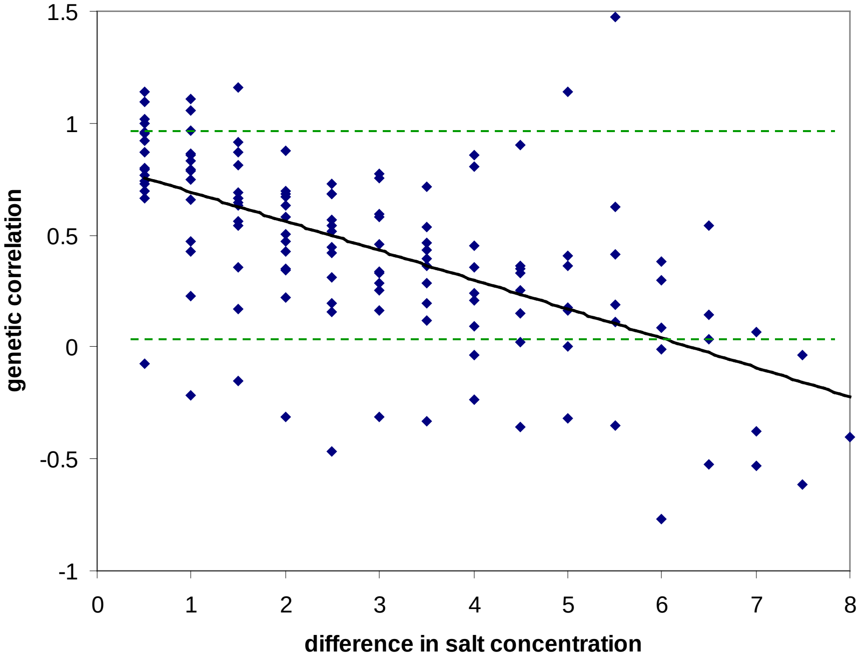


Moser & Bell 2010 in prep

The mechanism of adaptation to a deteriorating environment leading eventually to genocidal conditions

Adaptation to genocidal stress is the indirect response to adaptation at intermediate levels of stress experienced earlier in time.

This principle applies to every step in adaptation to a deteriorating environment, and is governed by the genetic correlation between successive conditions of growth. Hence, r_G should be larger when more similar environments are compared.



$r_G \rightarrow +1$ for very similar conditions

$r_G \rightarrow 0$ for very different conditions

Chase Moser: Chlamy/salt system

Evolutionary rescue in experimental cultures of wild yeast under salt stress

Pedram Samani (McGill)

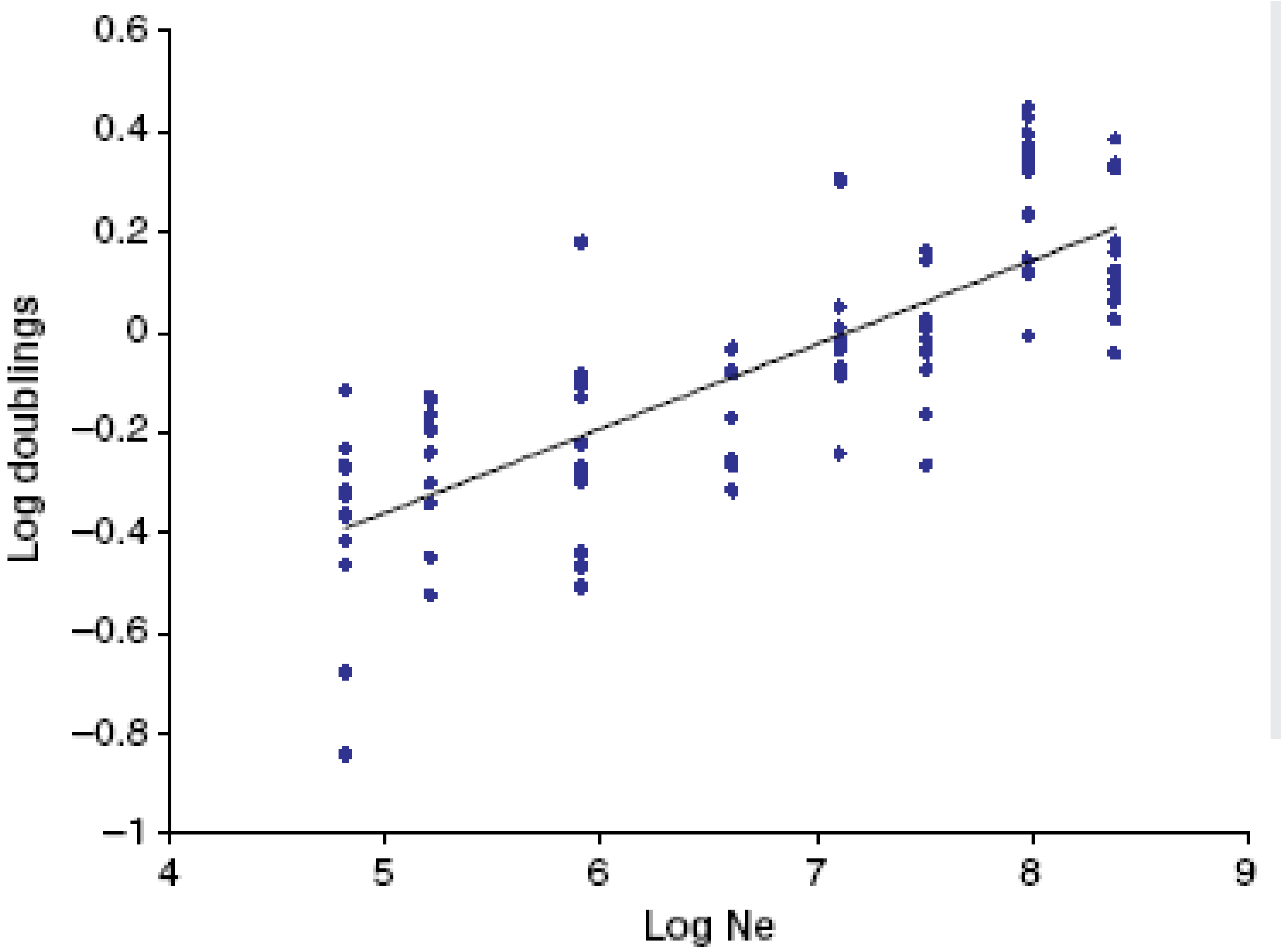


Fig. 3 Increase in doubling rate at 80 g L^{-1} NaCl in cultures of different volume at 45 g L^{-1} NaCl. Each point is a mean for each of 12 replicate lines, based on 200–300 colonies per line scored after the growth of 4 days. The regression is log doublings = 0.17 log *Ne* − 1.20, $r^2 = 0.62$ (d.f. = 90, $P < 0.001$). Note: Four aberrant plates from the fourth smallest treatment were excluded; if they are included, r^2 drops to 0.39 (d.f. = 94, $P < 0.001$).

Samani & Bell 2010 J Evol Biol (in press)

Robot arm moves
“landscapes” for
incubation and
measurement

Liquid-handling
station in flow hood
allows sterile
transfer of cultures

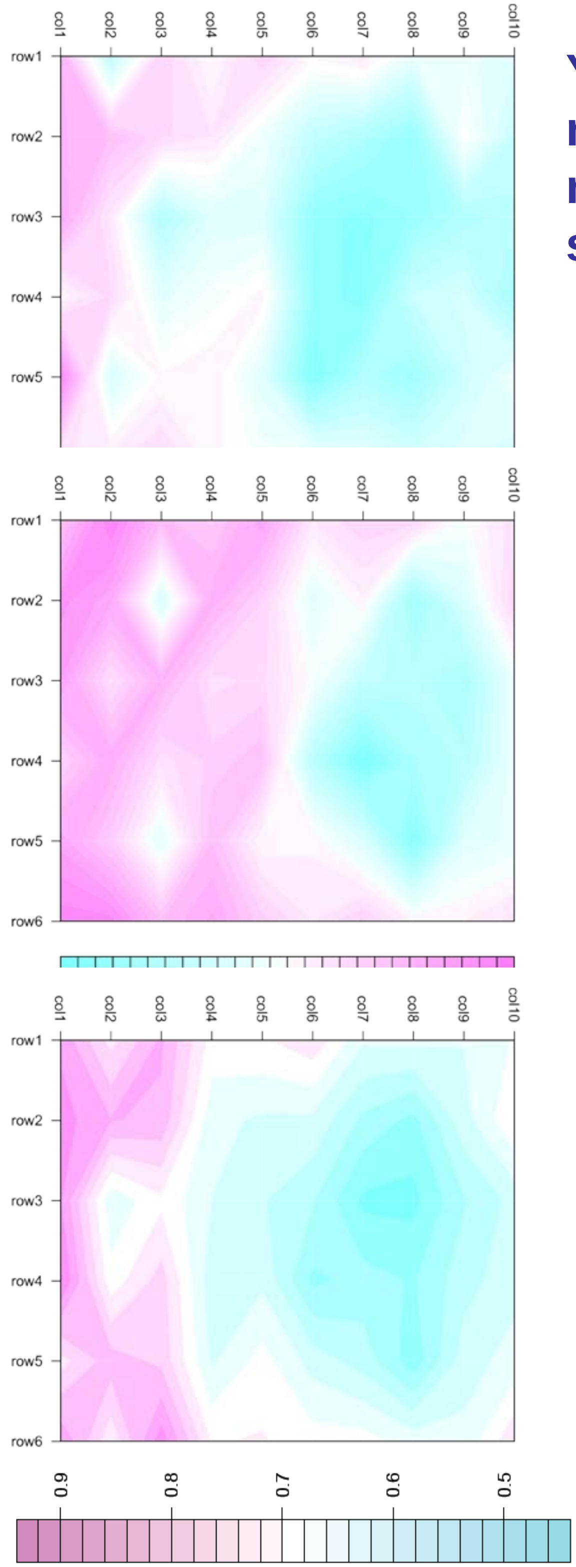
OD measurements
are automatically
downloaded to
central data
storage for the
experiment

Laboratory for Experimental Ecology and Evolution (LE3) at McGill

The Range Compression Experiment (RaCE)

8-pipette extraction, mixing and
inoculation gives precise
control of dispersal treatments

Model landscapes show how range is affected by environmental deterioration



Yeast/salt system. Heat maps of 96-well plate microcosms. Results for slow treatment.

No dispersal

Local dispersal

Global dispersal

Yield gradient

General conclusions

(or, what does this have to do with trees?)

❖Patterns of distribution may not accurately reflect local adaptation and specialization. It is essential to identify the characteristic spatial and phylogenetic scales before survey data can be interpreted.

❖The ecological and evolutionary responses to environmental change can be identified through evolutionary experiments with microbes.

❖Our results indicate that specific adaptation to elevated CO_2 is unlikely to evolve over a few hundred generations, although pronounced shifts in competitive relationships may occur.

❖The likelihood of evolutionary rescue depends on the rate and severity of change, the quantity of standing genetic variation, the rate of beneficial mutation and the pattern of local dispersal.

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- Our results indicate that specific adaptation to elevated CO_2 is unlikely to evolve over a few hundred generations, although pronounced shifts in community composition may occur.

- The likelihood of evolutionary rescue depends on the rate and severity of change, the quantity of standing genetic variation, the rate of beneficial mutation and the pattern of local dispersal.

- The long-term consequences of global change can only be identified through experiments using model ecological and evolutionary species and communities. These will usually be microbial.

General propositions that must be validated in order to transfer results from tractable systems to trees.

The relationship between characteristic distance (the spatial scale at which specific adaptation occurs) and individual distance is a constant for land plants.

The characteristic phylogenetic level (branching depth at which distinct ecological specialization occurs) is roughly constant for sexual clades.

Homologous physiological systems (such as photosynthetic pathways) respond to a given agent of selection in similar ways.

Bulk properties of the environment (such as the rate of deterioration) affect adaptation similarly in all organisms.

Bulk properties of the population (such as mutation supply rate) affect adaptation similarly in all organisms.

Technological advances that must be made in order to transfer results from tractable systems to trees.

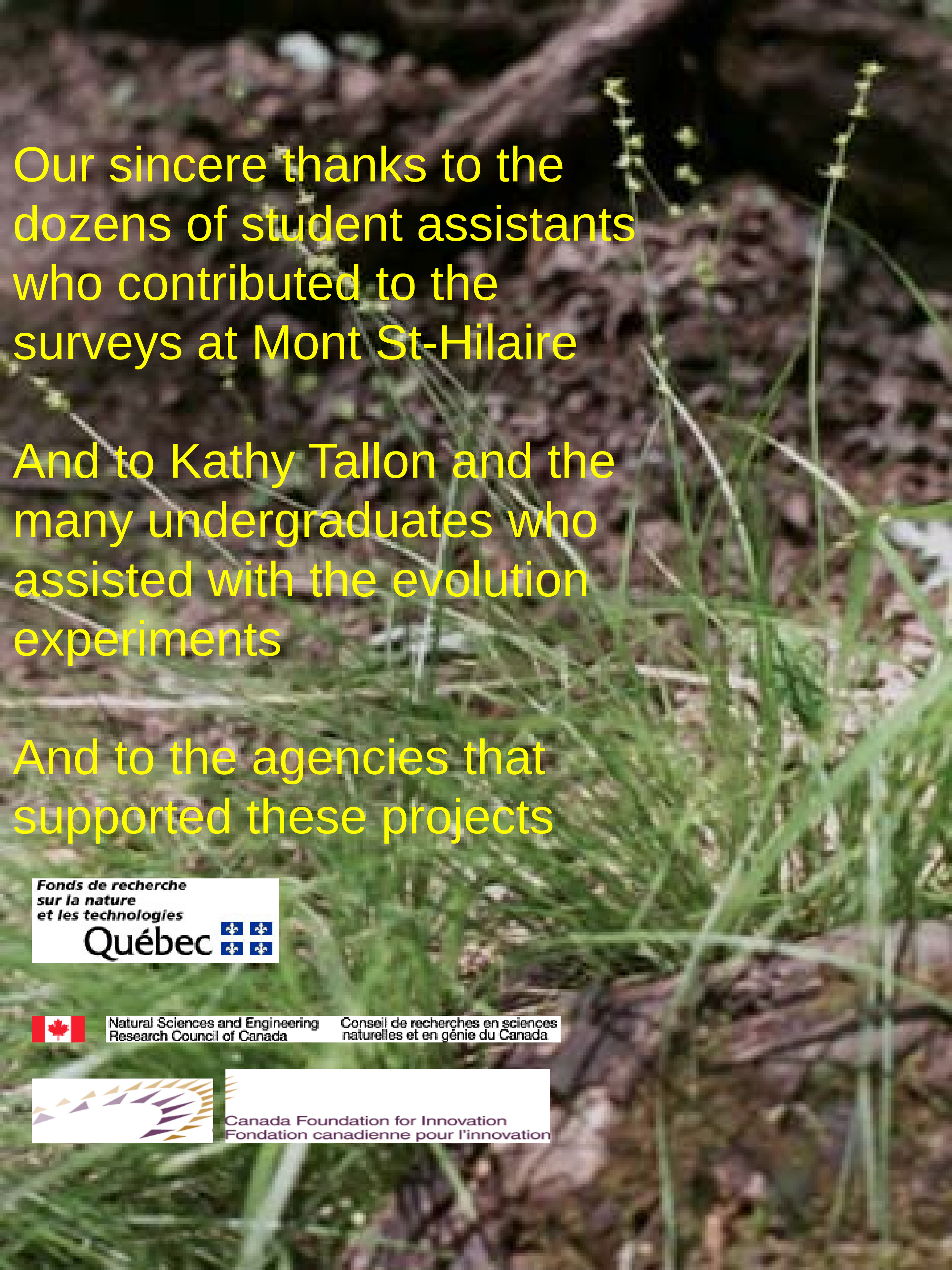
The widespread implementation of systematic biological surveys with appropriate spatial and phylogenetic scaling; and the storage of this information in standard format in a publicly accessible curated database.

The fabrication of experimental infrastructure capable of evaluating results obtained in smaller simpler systems to larger, more complex systems.

The construction of self-sustaining model communities with trophic structure capable of testing hypotheses concerning the response of complex evolvable systems to perturbation.

The ability to estimate food webs in natural communities using automated high-throughput procedures..

The development of bioinformatic tools for the standard analysis of biological surveys; and of mathematical or algorithmic methods for predicting the behaviour of complex evolvable systems.



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And to Kathy Tallon and the many undergraduates who assisted with the evolution experiments

And to the agencies that supported these projects

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sur la nature
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Research Council of Canada
Conseil de recherches en sciences
naturelles et en génie du Canada

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Fondation canadienne pour l'innovation