Fen diversity in the West Carpathians

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Mire ecology working group

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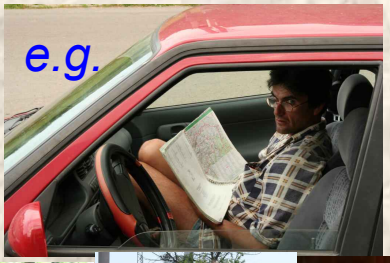


What is a fen?

Fen is a sedge-moss wetland, where carbon and nutrients are deposited into an organogenic material (peat, chalk or tufa). Vegetation is therefore nutrient-limited, adapted to water oversupply. Brown mosses (Bryidae) or sphagna are the dominant component, the share of specialists is high.

Distribution: boreal zone of Eurasia and North America, Patagonia

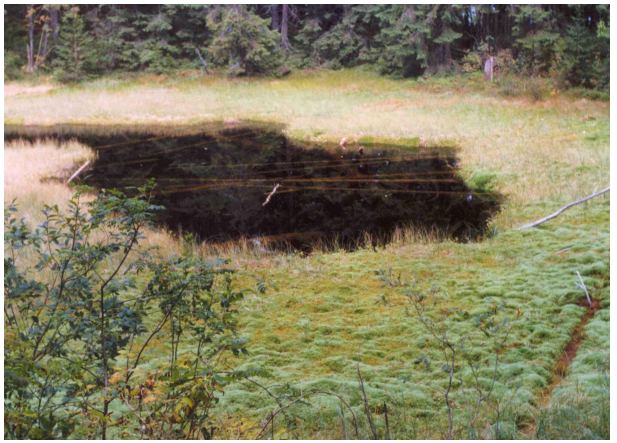
West Carpathians is the region where the calcareous fens are very common

Spring fens

Developed on springs, more common in the Carpathians

Topogenic fens

Developed by terrestrialisation, recently rare in the Carpathians



MIRE SUBDIVISION

Mire

Bog

Mixed mire

Fen

calcareous fen

rich fen

poor fen

= transitional mire

MIXED MIRE

a mosaic of bog hummocks and fens

Brown mosses

(*Calliergon, Scorpidium, Drepanocladus*)

Hummocks of *Sphagnum fuscum* and *S. rubellum*

West-Carpathian fens are distributed along the entire poor-rich gradient

What does it mean?

Calcium and pH correlate best with the major direction of floristic variation within mires worldwide. However, in many regions the complete base-richness gradient does not occur. In the West Carpathians, the complete gradient is available for various ecological studies.

Nevertheless, calcium and pH are not sole factors underlying the main floristic gradient:

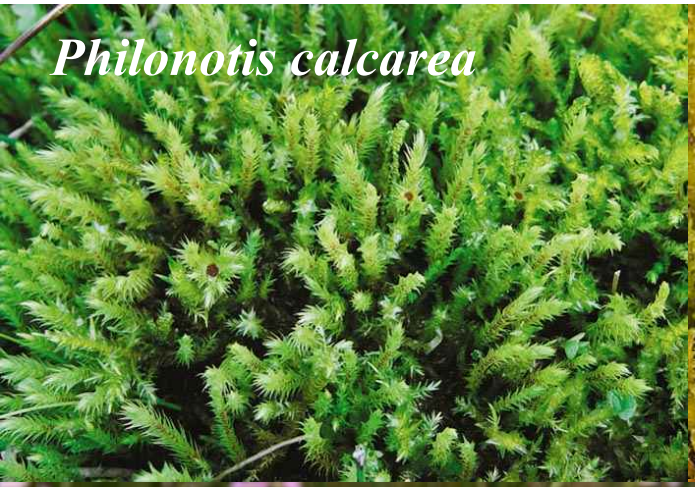
Extremely calcium-rich fens: deficiency of P (binded into calcite), ammonium ions (N-$NH_3^{+)}$, sometimes also deficiency of Fe and K (mown habitats). Toxicity of minerals. Low content of free CO_2 in water for moss photosynthesis.

Extremely calcium-poor fens: toxicity of Fe, Mn and Al, deficiency of Ca a Mg for some calcicole plants, deficiency of nitrate, strong competition of sphagna.




Along the poor-rich gradient, species composition steeply changes. We can distinguish six habitats, clearly delimited by plant or animal species.

Calcareous fens (*Caricion davallianae*): Tufa formation! Very rare in the boreal zone of Eurasia.


Philonotis calcarea


Cratoneuron commutatum


Eriophorum latifolium
© P.Hájková


Primula farinosa


Drepanocladus cossonii


Pinguicula vulgaris
© P.Hájková

Along the poor-rich gradient, species composition steeply changes. We can distinguish six habitats, clearly delimited by plant or animal species.

Calcareous fens (*Caricion davallianae*): include a very **unique habitat with halophytes** (Spiš and Liptov basins).

Distribution: Spiš basin (e.g., Hôrka, Gánovce), Liptov basin (e.g., Stankovany)
Either on isolated small waterlogged springs or at the margins of travertines

Gánovce

Hôrka

It is difficult to find analogy of these salt-rich calcareous fens in the world.

Similar co-existence of fen and halophilous species occurs in some Central-Asian salt-rich fen grasslands (Altay Mts – photo)

Analogies: *Trichophorum pumilum, Eleocharis quinqueflora, Carex dioica, Glaux maritima, Pedicularis palustris, Triglochin maritimum, T. palustre*, *Primula nutans (farinosa* group*), Parnassia palustris, Dactylorhiza salina*...

More widespread habitat during dry phases of the Pleistocene?

Zonation of a fen close to Aktash

? analogy of Late-Glacial in the W.C.

mixture of fen and salt-tolerating species at an edge

Calliergon trifarium →

Eleocharis quinqueflora

Blysmus rufus →

Parnassia palustris →

Gentianopsis barbata →

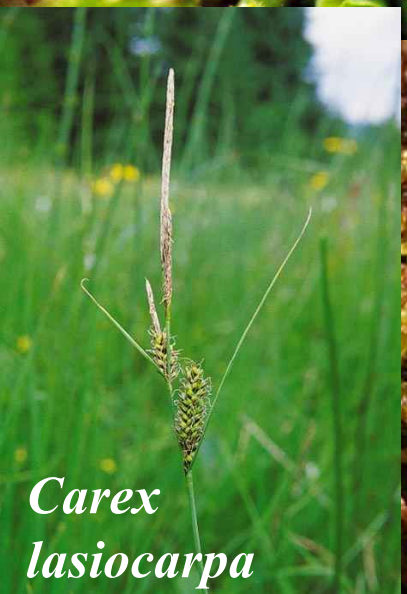
Puccinelia species →

Cirsium esculentum

Halerpestes salsuginosa →

Extremely rich fens (*Caricion davallianae,*

Caricion lasiocarpae sensu Rybníček 1984): not tufa-forming, but rather peat-forming ecosystems. Still no sphagna occur.



Vegetation composition and structure differ strongly between tufa-forming fens and peat-forming calcareous fens.

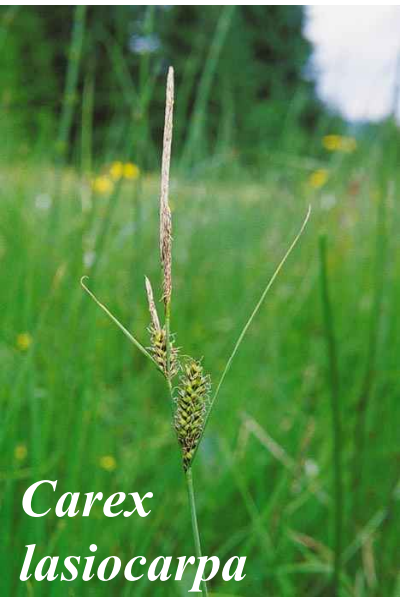
Carici flavae-Cratoneuretum;
Bílé Karpaty ←

Valeriano-Caricetum flavae,
Levočské vrchy →

Rich fens (*Sphagno warnstorfii-Tomenthypnion*, incl. *Caricion demissae* sensu Rybníček 1984): High species richness due to coexistence of calcium-tolerant sphagna and calcicoles

E. latifolium

Sphagnum warnstorfii *Sphagnum contortum*



S. contortum

S. subnitens

S. warnstorfii

S. obtusum

Calcium-tolerant sphagna co-exist with brown mosses

S. teres

Rich fens include

(a) waterlogged habitats with boreal species *Carex lasiocarpa, C. chordorrhiza, C. diandra, C. limosa, C. pulicaris*. In the boreal zone this habitat is often wooded

(b) mown fen grasslands with meadow broadleaved species and grasses.

Sphagno warnstorfii-Caricetum lasiocarpae, Sweden

Sphagno warnstorfii-Eriophoretum latifolii, Beskydy

History

The Late-Glacial samples from Carpathian calcareous and rich fens showed that bog woodlands with *Pinus sylvestris, Picea Abies, Salix* and *Alnus* co-existing with calcium-tolerant *Sphagna* (*S. teres*) and small sedges formed initial phases of peat formation.

Similar habitats occurred even in the Late-Glacial phases of some recently strongly calcareous fens (Rojkov, Rakša)

Analogy

Bog woodlands in southern Siberia with e.g. *Helodium blandowii, Pupilla alpicola ....*

see also poster of Petra Hájková

Moderately rich fens (*Caricion fuscae*): calcium-tolerant sphagna can still occur, but calcicole specialists are missing. On the other hand, no ombrotrophic-bog species and no dominance of *Sphagnum* Sect. *Cuspidata* or *Palustria* occur.


Sphagnum auriculatum


Hydrocotyle vulgaris


Aulacomnium palustre


Carex lasiocarpa

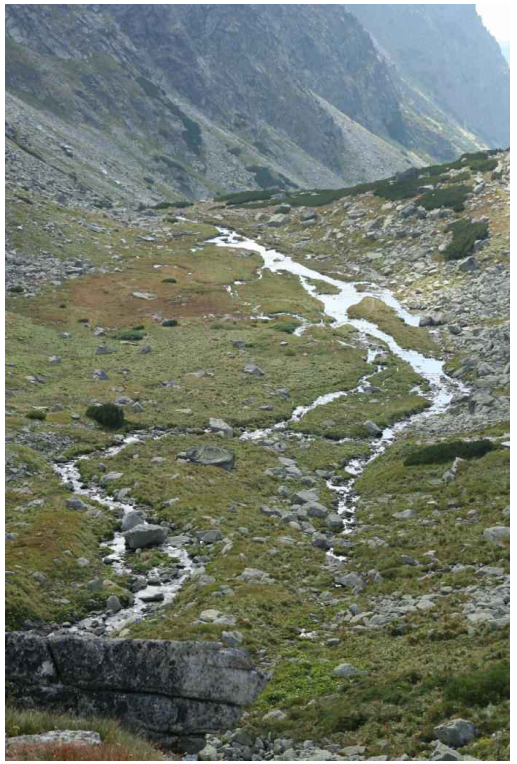

Sphagnum teres


Carex nigra


Eriophorum angustifolium

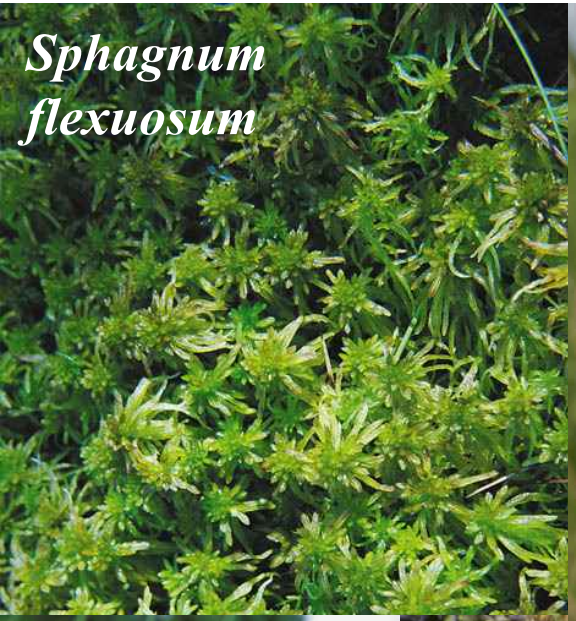
Moderately-rich fens include:

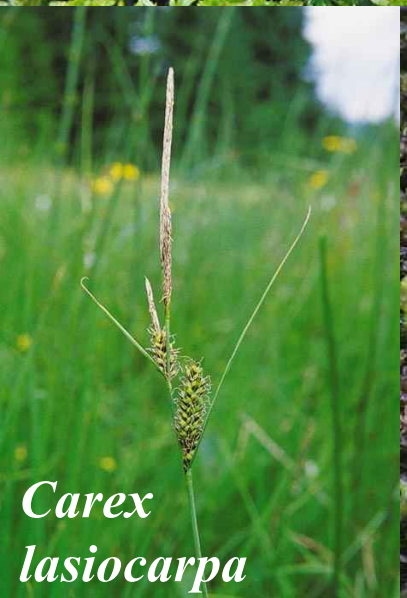
a) small high-mountain fens with *Drepanocladus exannulatus*



b) young fen grasslands, managed

Poor fens (*Sphagno recurvi-Caricion canescentis*): still fed by groundwater, but extremely mineral-poor. Nutrient concentrations (N, P, K) and pH are higher than those in ombrotrophic bogs. Dominance of sphagna.





Poor fens include terrestrialised ponds as well as young managed fen grasslands.

Carici rostratae-Sphagnetum recurvi caricetosum limosae

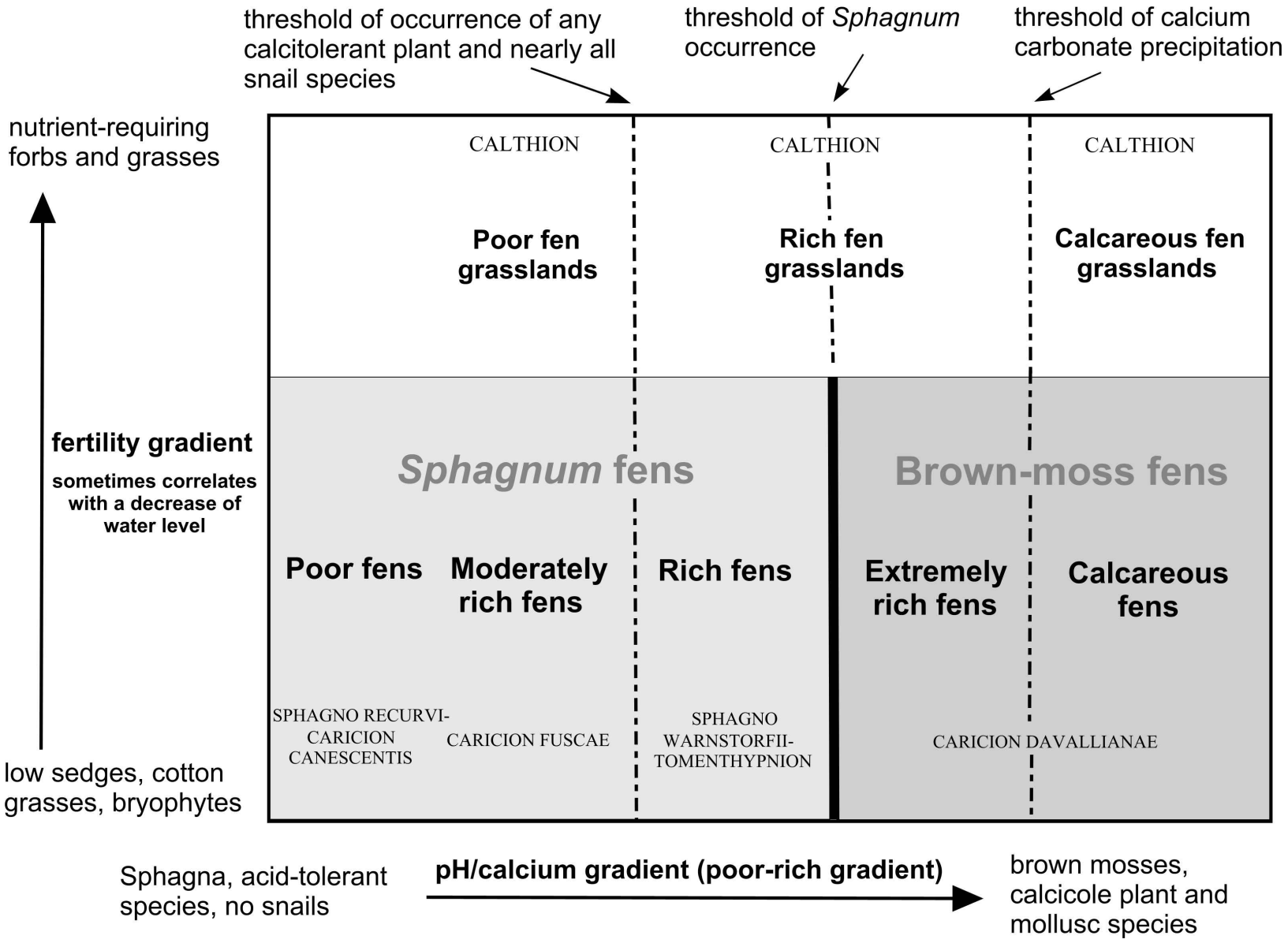
Carex magellanica at the Surdíky fen

Carici echinatae-Sphagnetum recurvi

Recently they are spreading due to *Sphagnum flexuosum* and *S. fallax* invasions into rich fens.

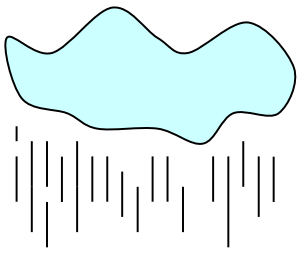
It is hypothetised that this succession is accelerated by P-enrichment.

Summary of fen classification

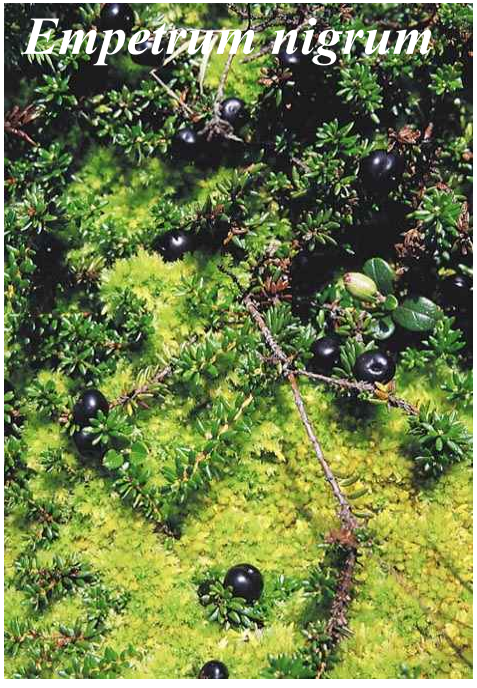


Ombrotrophic bogs: contrary to fens they are fed exclusively by rainwater, they are poor in broadleaved herbs, grasses and sedges


Sphagnum magellanicum




Eriophorum vaginatum


Empetrum nigrum

Although described ecological patterns explains much diversity in the West-Carpathian fens, a great share of variability is attributed to

biogeographical patterns

1. **Different history of Outer and Inner Carpathian fens causes differences in species composition – some fen species are confined to Inner Carpathians where fens have an older history**

see poster of *Petra Hájková* and lecture of *Michal Horsák*

widespread ——— *partially spatially structured* ⟶ *only paleorefugia*

⟵ *? dispersal ability ?* ⟶

2. Historical distribution of particular habitats is mirrored in recent species composition and richness

Theory: Historically more common habitats have evolved a larger pool of adapted species and therefore are richer in species.

Theory: Bimodal distribution of water pH across mires due to buffer systems. It should be a stable phenomenon in time.

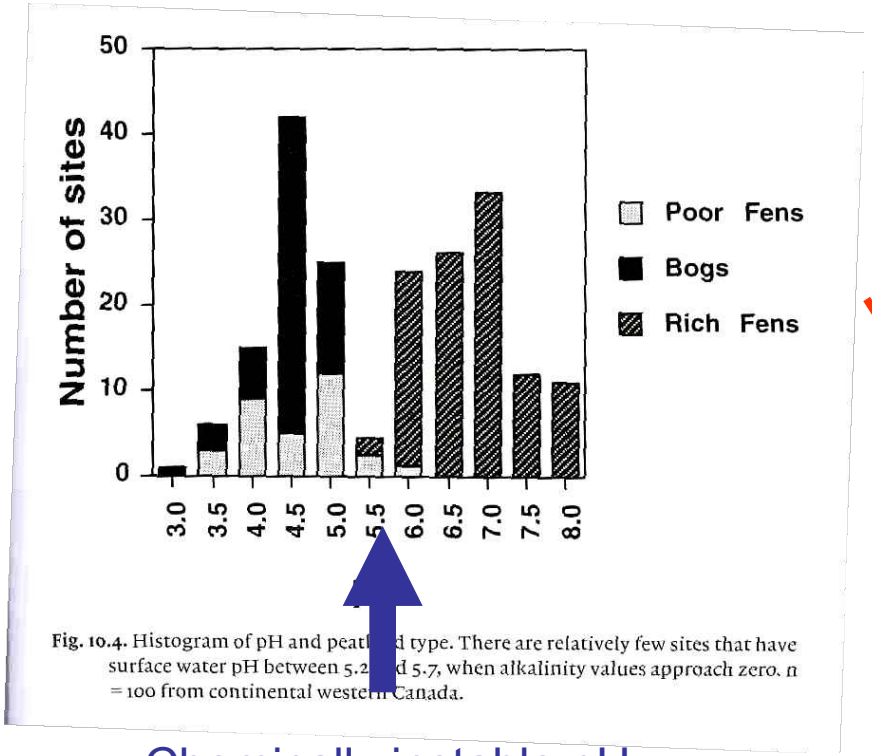
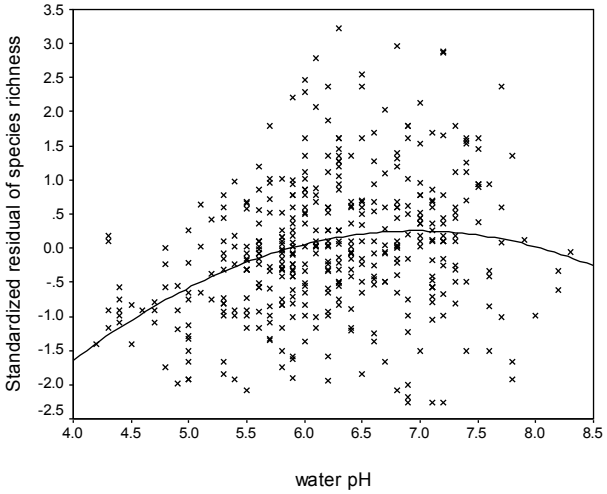


Fig. 10.4. Histogram of pH and peat[illegible]d type. There are relatively few sites that have surface water pH between 5.2 [illegible]d 5.7, when alkalinity values approach zero. n = 100 from continental weste[illegible] Canada.

Chemically instable pH, rare in evolutionary time

Reality:

species richness pattern is linear or unimodal



Possible explanation of this discrepancy: historically common habitats are rich in pH specialists, while total species richness is influenced by generalists

Phytosociological support for this explanation:

***Oxycocco-Sphagnetea*:** ombrotrophic bogs, low pH, low species richness, but high number of diagnostic species (specialists)

Caricion fuscae (fen meadow developed under human impact): pH between 5.5 and 6.0, thus unstable and historically rare; high species richness, but low number of diagnostic species - specialists.

Example: *Drepanocladus exannulatus* is diagnostic for this vegetation. It has optimum at pH 5.4-5.6 and the same value is found accross regions. But this species has always very wide realised niche with respect to pH!

***Caricion davallianae*:** calcareous fens, high pH, lower number of species in vegetation plot as compared to *Caricion fuscae*, but high number of diagnostic species (specialists)

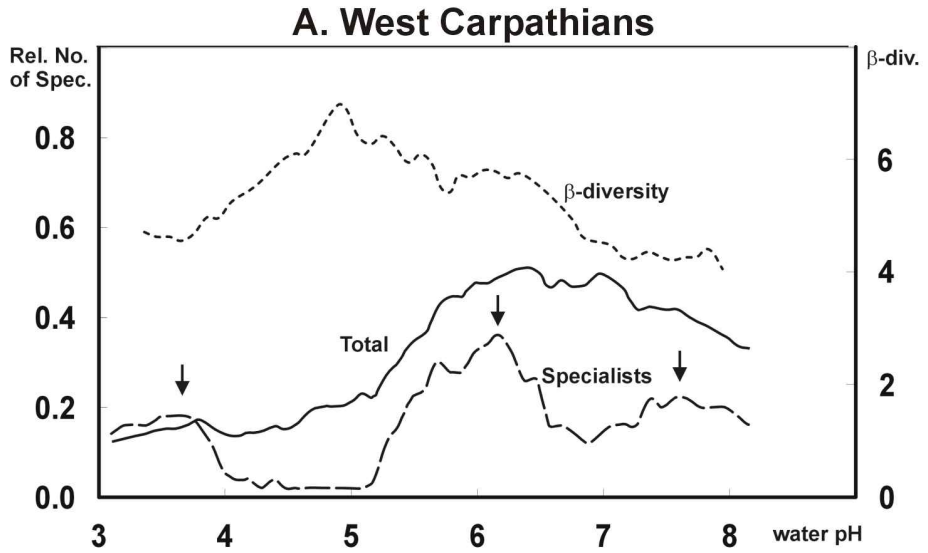
Result of our study:
Species pool of specialists changes unevenelly along the pH gradient

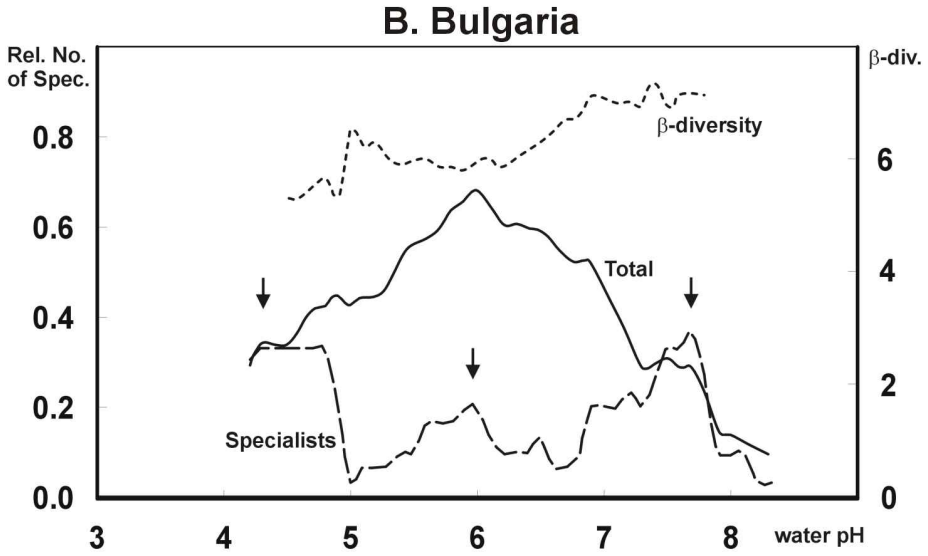
Confirmed prediction:

Uneven distribution of pH specialists along the pH gradient

Surprising result:

Three peaks instead of two (as would be suggested by bimodal distribution of pH due to buffer systems)



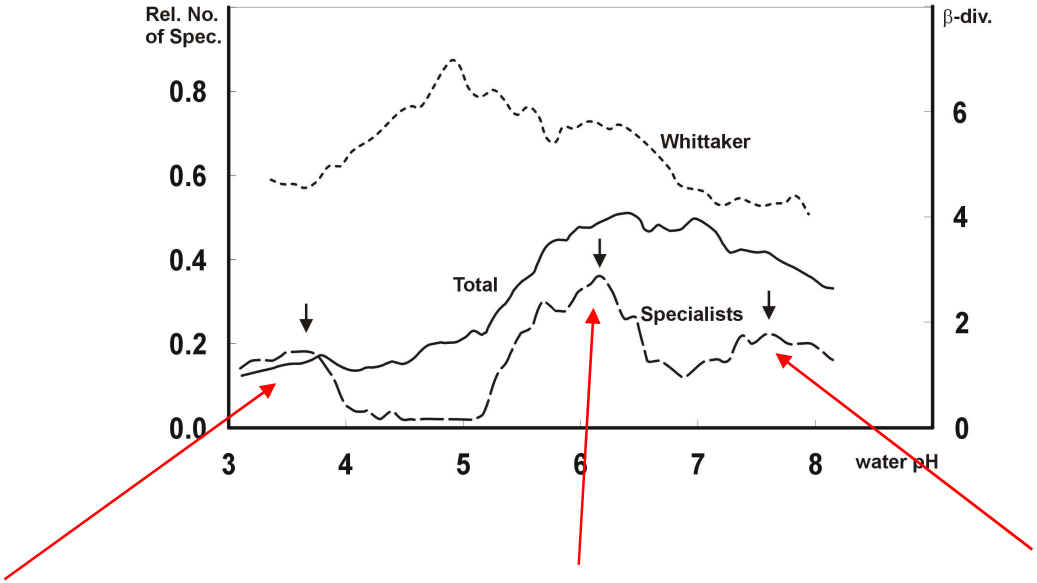


Possible interpretations of the trimodal specialist distribution

Hydrochemistry in evolutionary time

Bimodal distribution of pH in mires is not consistent across different regions and three modes have been common through evolutionary time.

Refugial history



Ombrotrophic conditions

Known from Preboreal in the W.C. (Belanské lúky)

Minerotrophic conditions, but low Ca concentration (peat-forming)

Known from the Full-Glacial in the West Carpathians

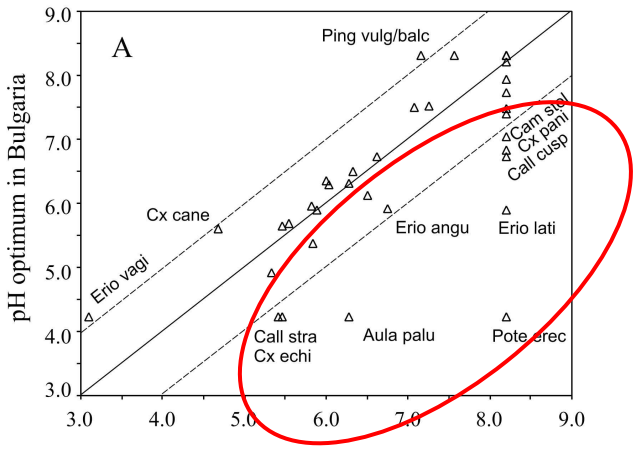
Minerotrophic conditions on limestones and marls (tufa formation)

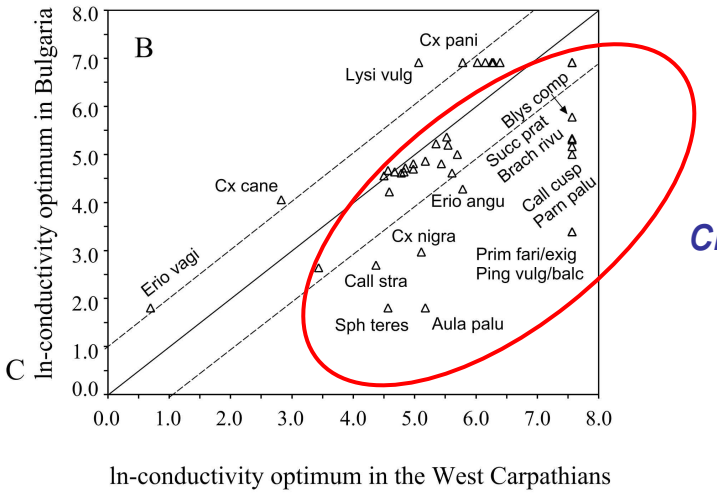
Known from the Late-Glacial in the Inner West Carpathians

3. Great commonnes of calcareous refugia in the West Carpathians led to ecotypic adaptation within species

comparison of West Carpathians (mostly calcareous refugia) and Bulgaria (mostly acidic refugia)

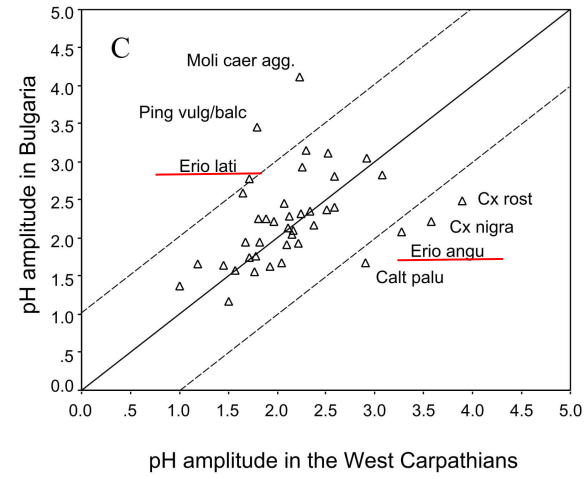
optimum

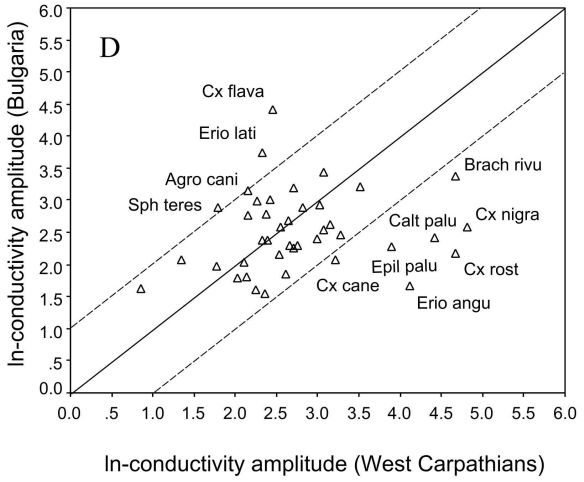




clear trend

amplitude





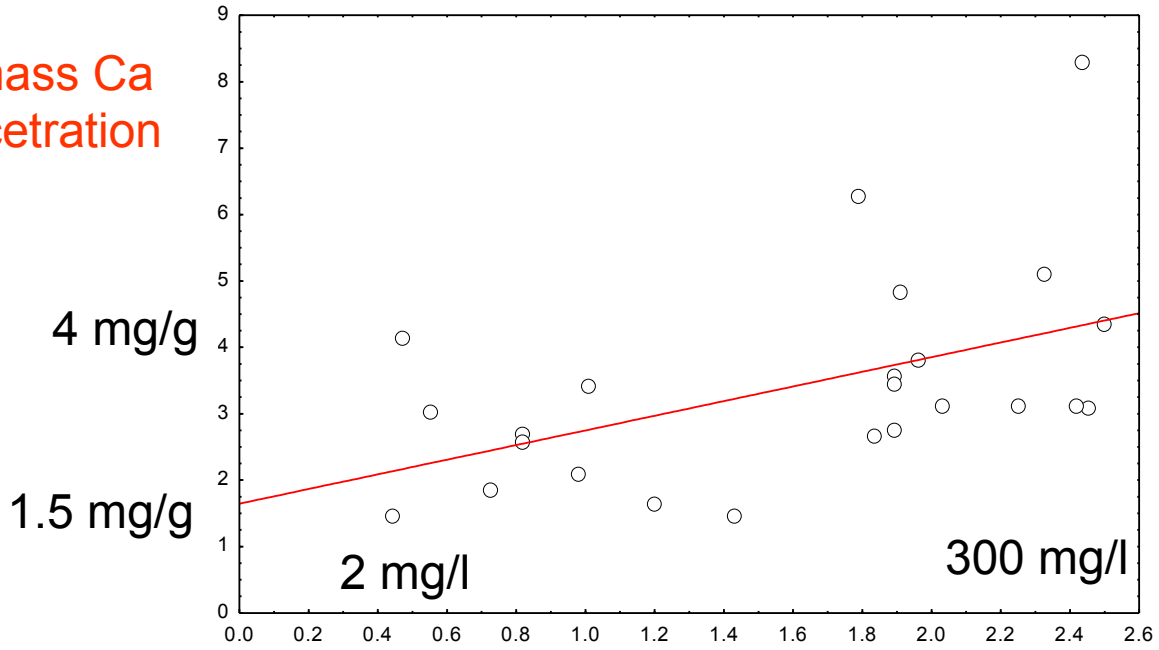
no trend

3. Great commonnes of calcareous refugia in the West Carpathians led to ecotypic adaptation within species

The most fragrant example:

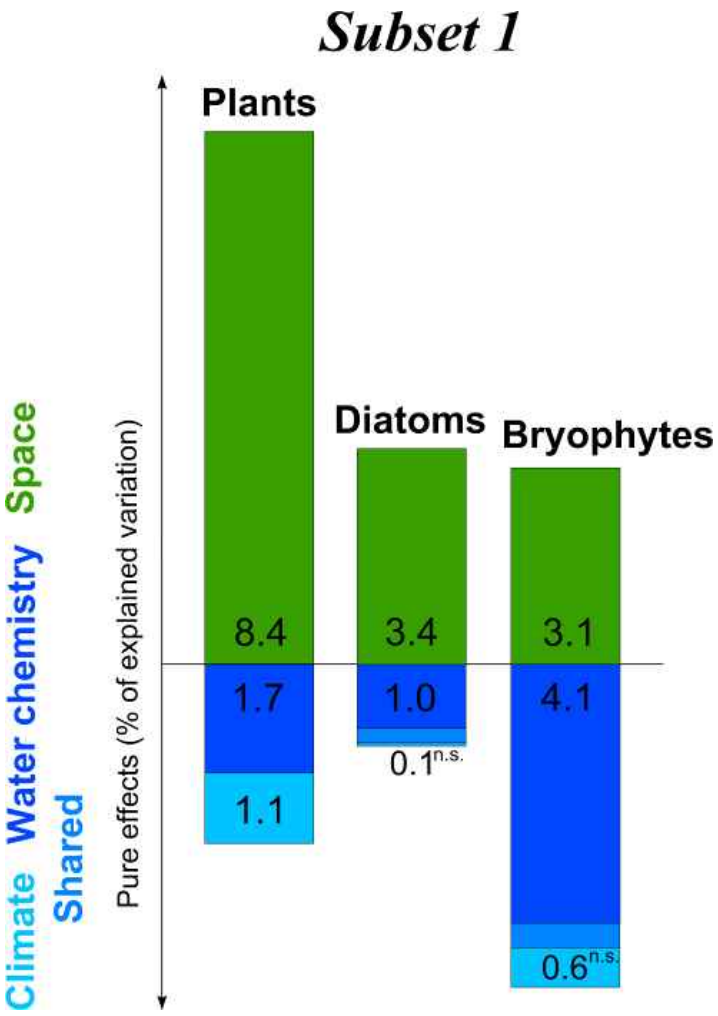
In the West Carpathians, *Eriophorum angustifolium* is common and even dominating in tufa-forming calcareous fens, while in other European regions this species characterises the most acid habitats.

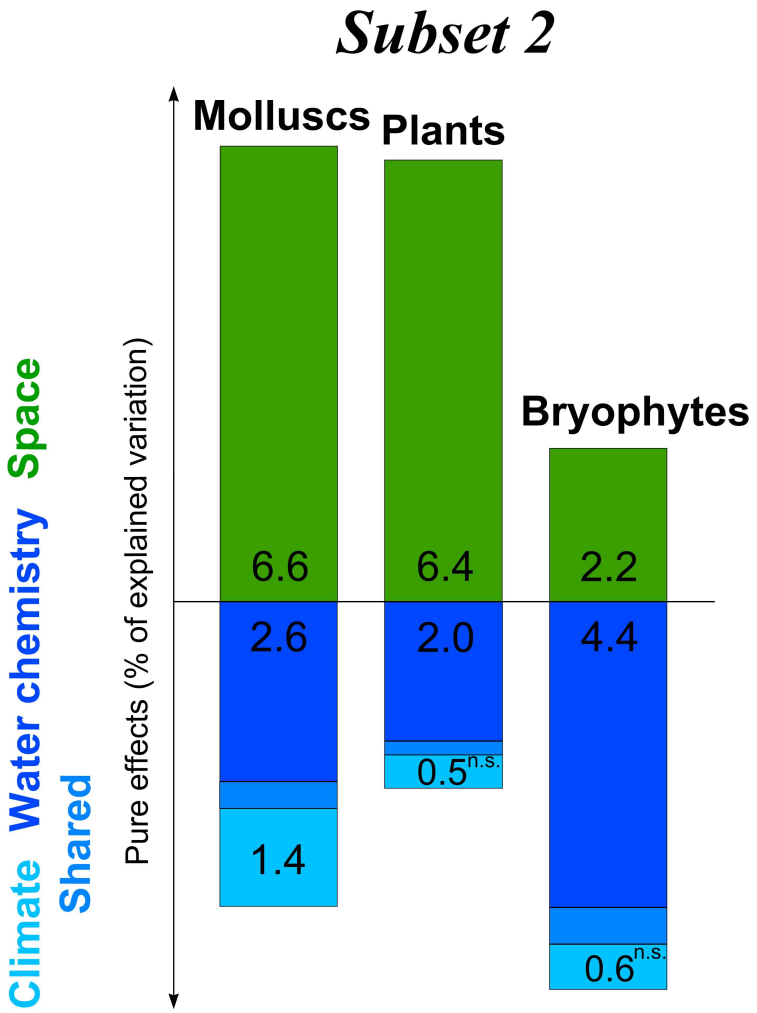
Presumed principle of this local adaptation – rather low uptake of Ca in Ca-rich habitats. The species have much lower Ca-concentration in tufa-forming fens than other species (Rozbrojová & Hájek *in press.*)



4. Different dispersal ability of different taxonomic groups shapes distribution patterns

Relative effects of water chemistry (pH, conductivity) versus geographical position (PCNM axes)





5. Migration routes – subatlantic migrants stopping at NW edge of the Carpathains

Lycopodiella innundata

CONCLUSIONS

1. Water pH and calcium richness are major determinants of species composition in West Carpathian fens; their effect is either direct or mediated through nutrient availability, iron toxicity, or structure (dominance of *sphagna*)

2. Distinct habitats, characterised by specific species combinations, can be distinguished along this gradient

3. Historical factors such as „refugial biogeography“ contribute to explain recent species composition of fens