Changes in biodiversity: are there general implications for ecosystem functioning?

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Why are functional effects of diversity not ubiquitous ?

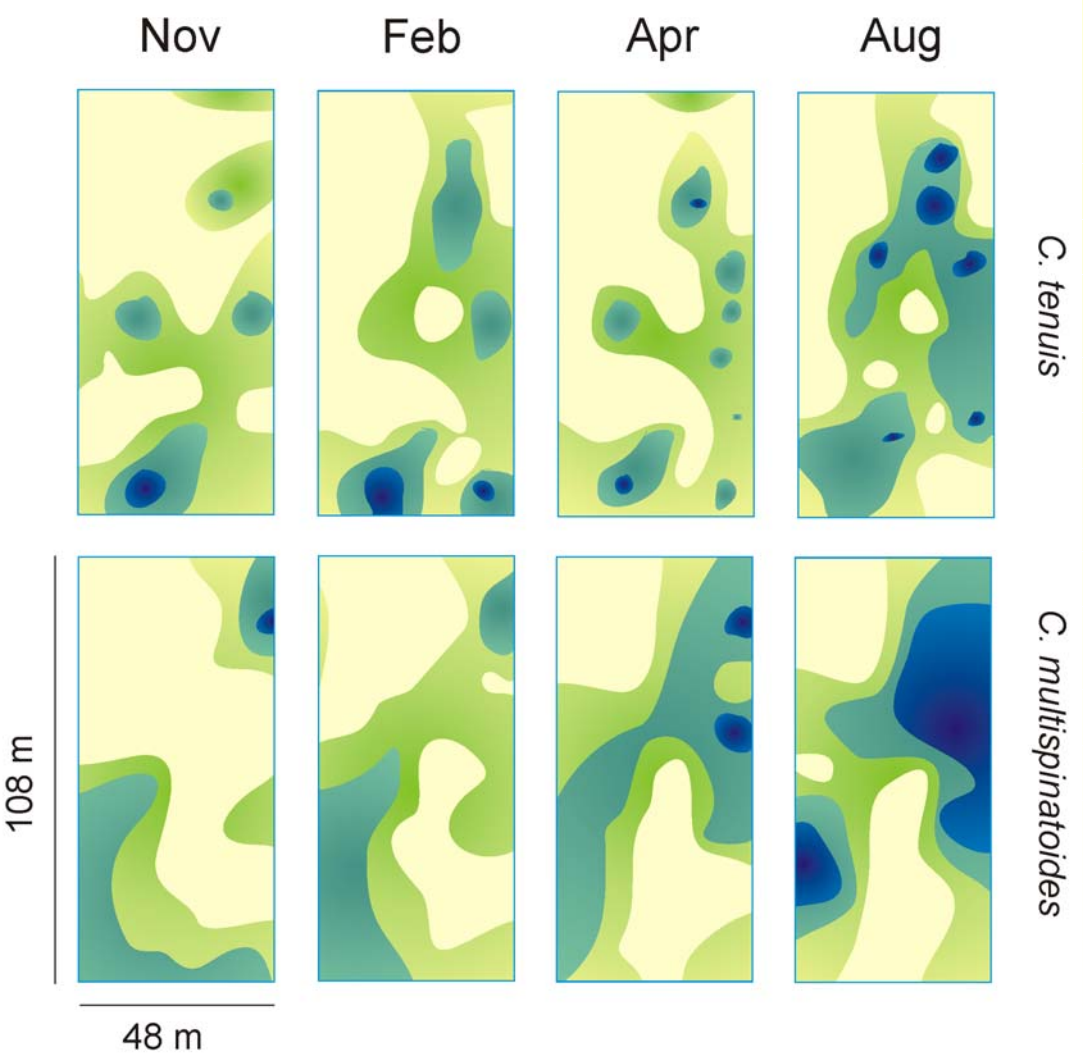
Can we predict whether diversity effects are likely to occur under particular circumstances ?

1. Hypotheses

2. Predictions

3. Empirical evidence

Complementary abundance in space and time



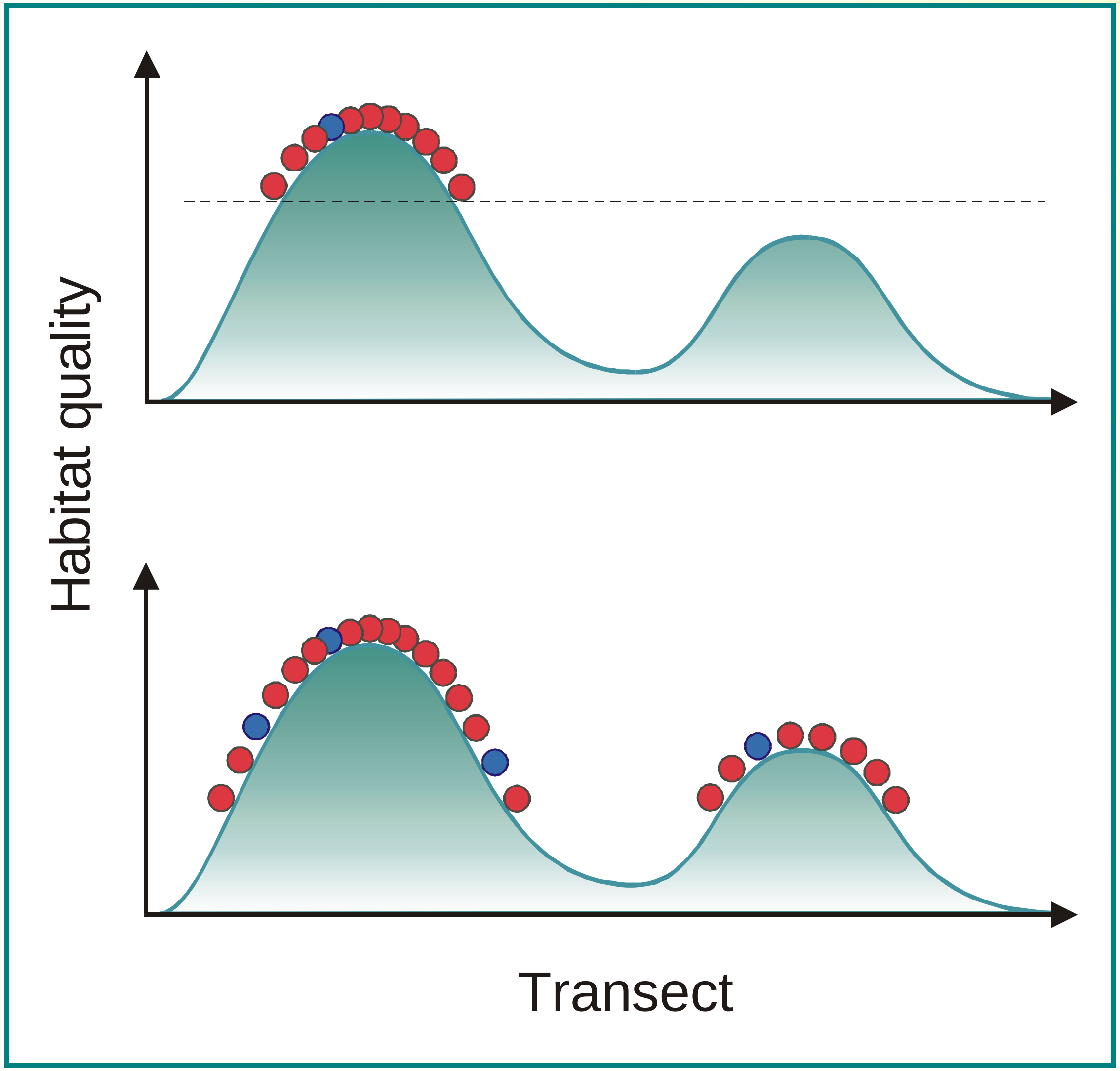
Nematode communities
(Chronogaster species)
in a riparian wetland
(Ettema et al. 2000)

Hypothesis 1:

In a rich community, asynchronous spatio-temporal fluctuations of species compensate each other, which leads to less variation and to higher average biomass in a species-rich community than in a species-poor community.

Ideal Free Distribution Theory

(Fretwell and Lucas 1970, Milchtaich 1996)



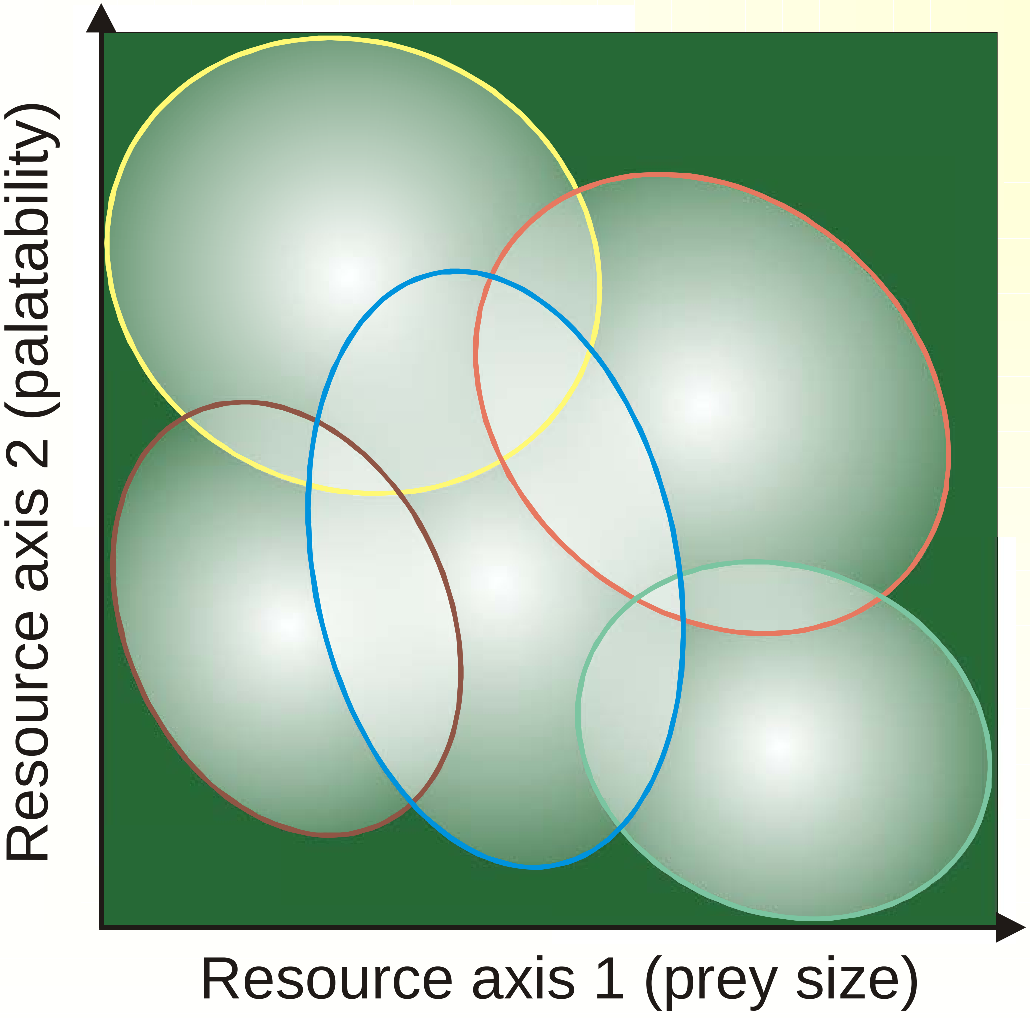
Counter-Hypothesis 1b:

Ideal Free Distribution Theory predicts that organisms will re-locate continuously to exploit the most suitable parts of the habitat, dependent on total abundance, but independently of species richness.
Ideal Free Distribution Theory is limited to the spatial scale up to which the organisms can orientate (= perceive + dislocate).
It does not apply to sessile organisms.

List of Hypotheses (1)

Effect-type	Richness effect expected No	 Yes	 Scale-dependent
Reduced variance in space and time (due to levelling-out of fluctuations)	Motile organisms	Sessile organisms	Space (Time)

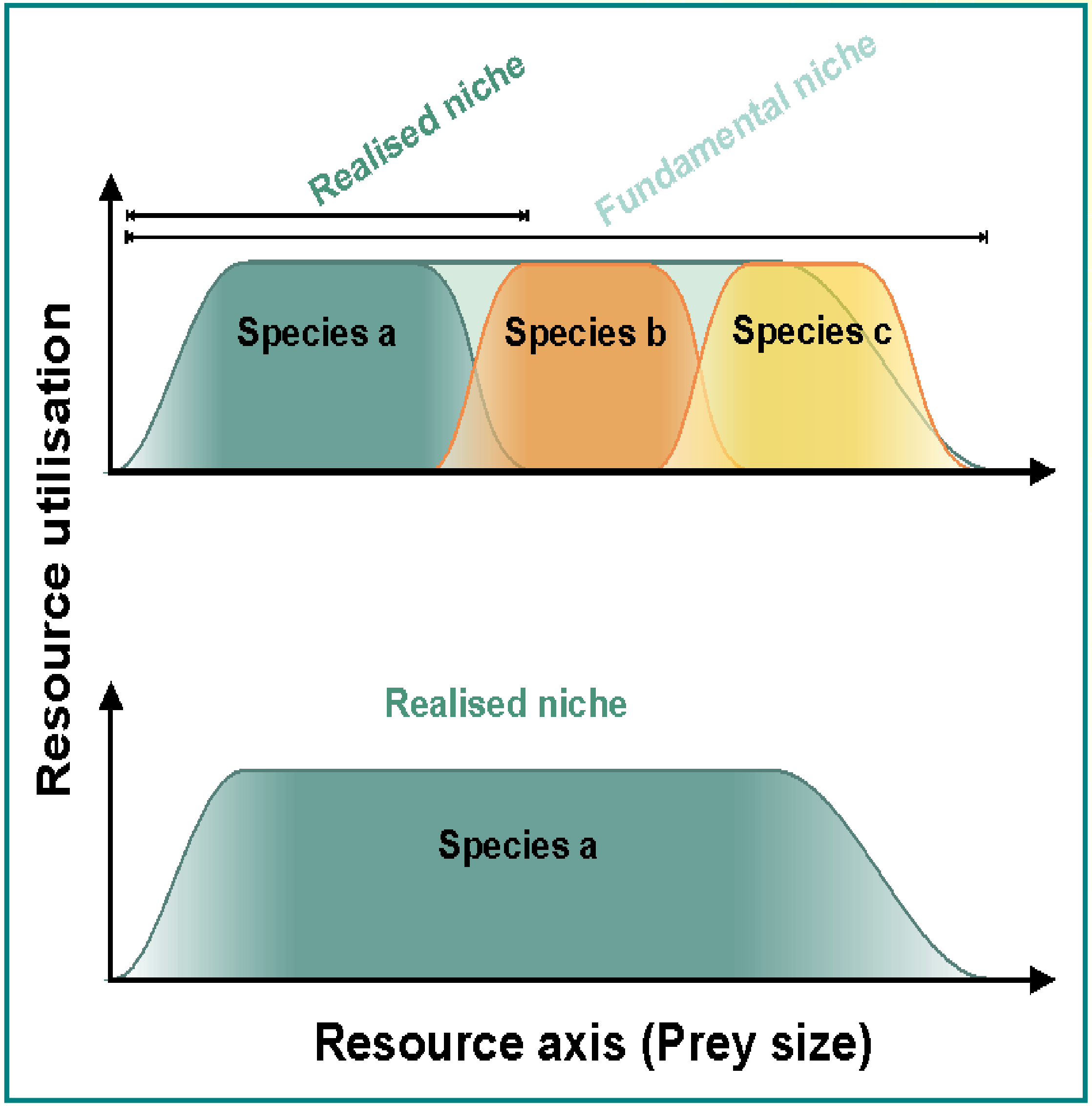
Complementary resource utilisation



Hypothesis 2:

In a rich community, niche overlap leads to a more complete exploitation of resources, and therefore to a higher community standing crop, than that of a species-poor community.

Competition Theory



(MacArthur & Wilson 1967)

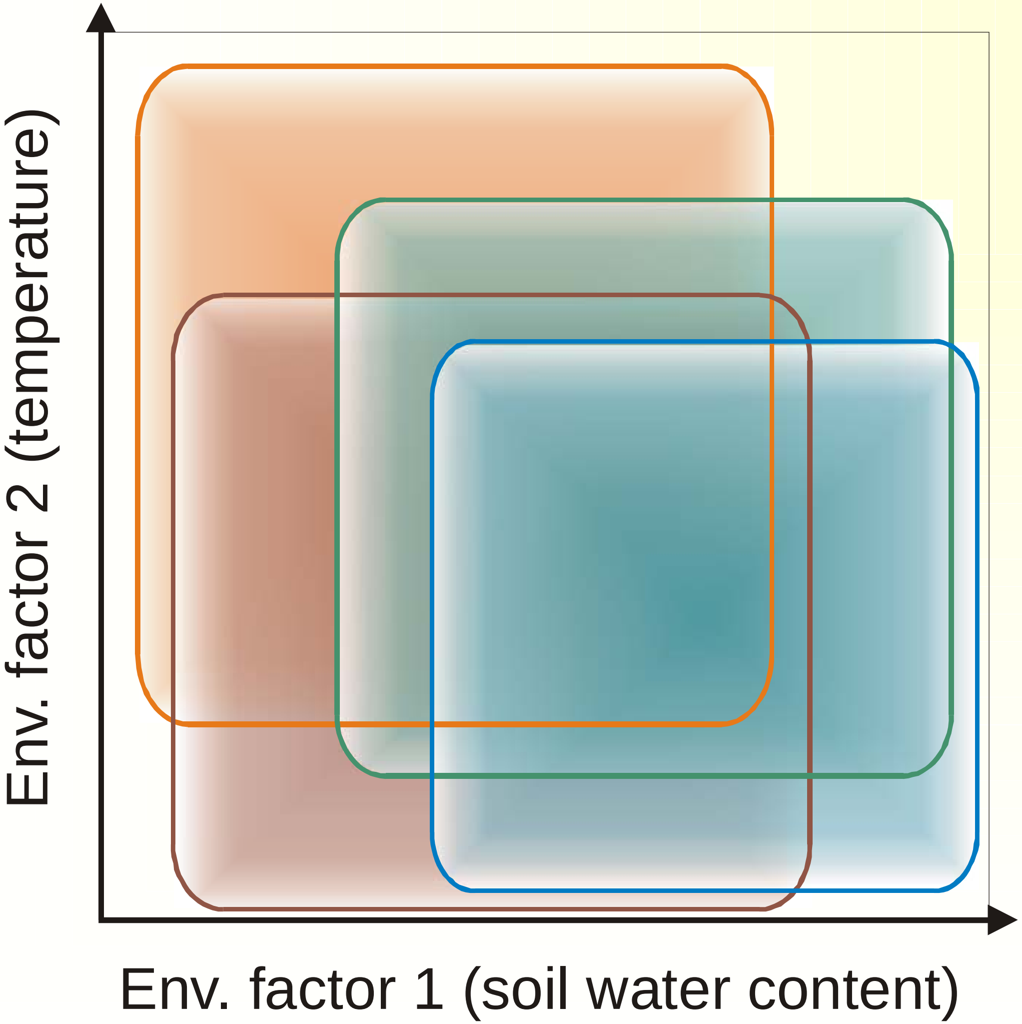
Counter-Hypothesis 2b:

Competition Theory predicts that competition release will invoke niche expansion, enabling a species-poor community to use the same resource spectrum as a species-rich community. Richness effects will only occur in communities where fundamental niches are largely disparate. This is likely to occur in communities with few species.

List of Hypotheses (2)

	Richness effect expected		
Effect-type	**No**	**Yes**	**Scale-dependent**
Reduced variance in space and time (due to levelling-out of fluctuations)	**Motile organisms**	**Sessile organisms**	**Space (Time)**
Intensified habitat exploitation (due to complementary resource utilisation)	**Species-rich communities**	**Species-poor communities**	**Transitory in time**

Complementary tolerance ranges

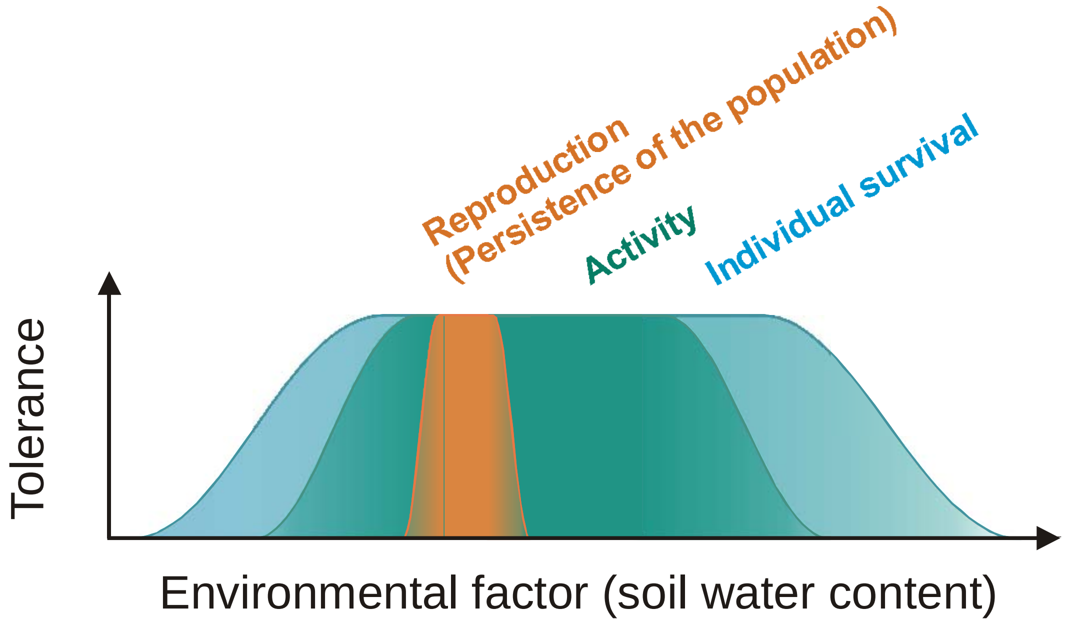


<u>Hypothesis 3:</u>

There is a higher probability in a species-rich community than in a species-poor community for at least one species being able to tolerate occasional extreme conditions (Spare Wheel Hypothesis). This leads to fewer interruptions of community activity and hence to a higher average of a communitie's total activity over time.

Ecophysiology

(Mackenzie et al.1998)



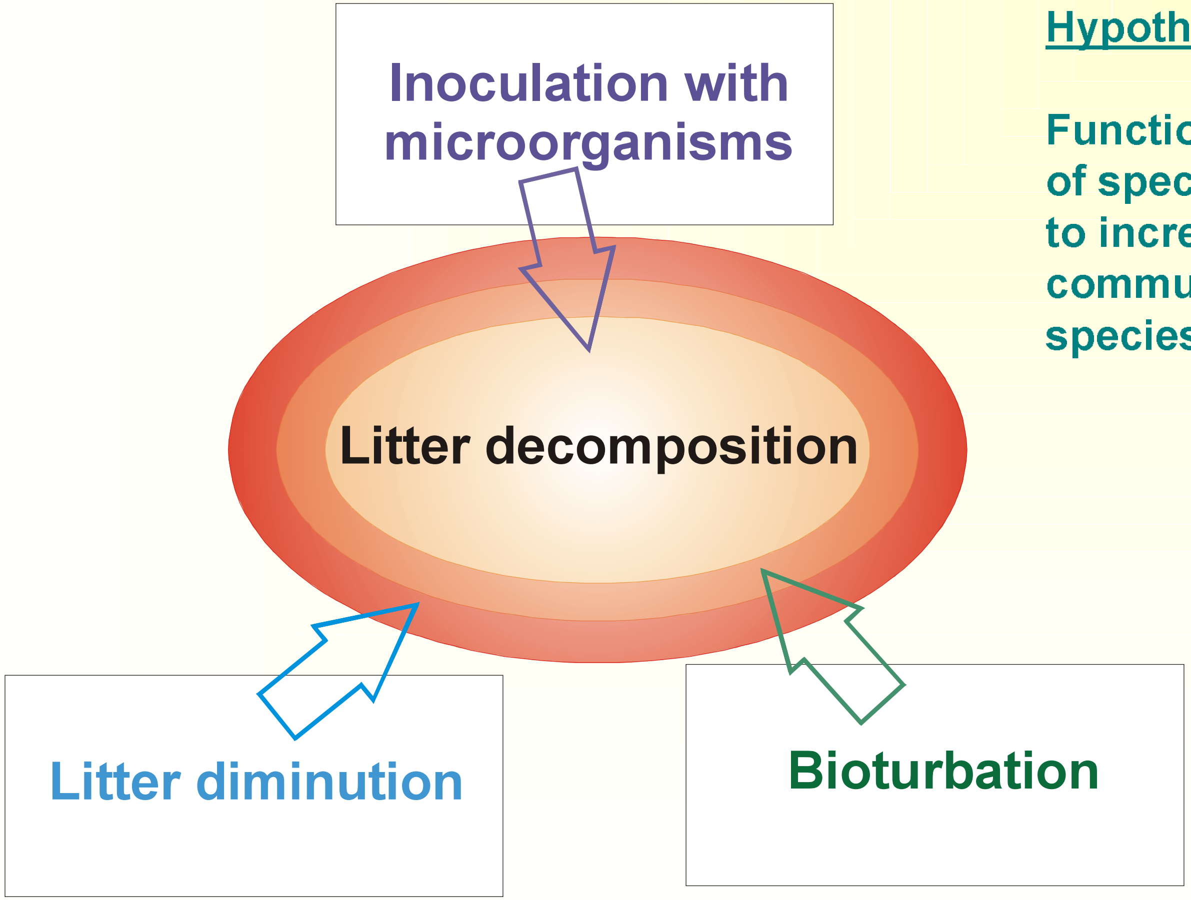
Counter-Hypothesis 3b:

Ecophysiology states that tolerances for survival, activity and reproduction are generally different and typically nested. Therefore, habitat properties can at the same time restrict persistence of populations while not affecting activity of persisiting populations. In this case, there will be no richness effects on community activity that are dependent on tolerance.

List of Hypotheses (3)

	Richness effect expected		
Effect-type	**No**	**Yes**	**Scale-dependent**
Reduced variance in space and time (due to levelling-out of fluctuations)	**Motile organisms**	**Sessile organisms**	**Space (Time)**
Intensified habitat exploitation (due to complementary resource utilisation)	**Species-rich communities**	**Species-poor communities**	**Transitory in time**
Higher average activity (due to complementary tolerances)	**Organisms with differing tolerances for reproduction and activity**	**Organisms without decoupling of reproduction and activity**	

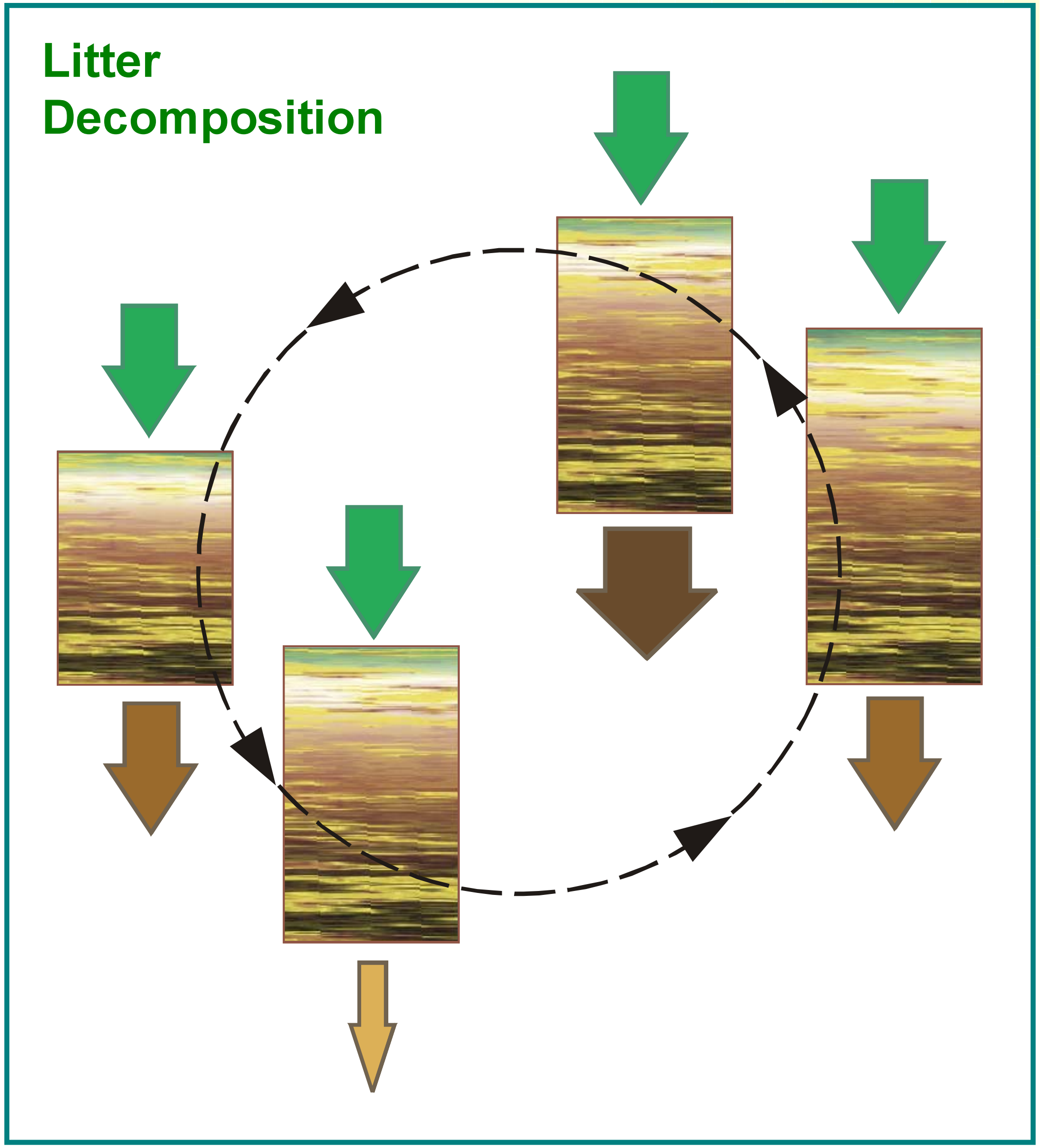
Functional synergy



Hypothesis 4:

Functional complementarity of species' activities leads to increased intensity of community function in a species-rich community.

Flow equilibrium



(Zheng et al. 1997)

Counter-Hypothesis 4b:

Dynamic Equilibrium Theory states that changes in process rates will be compensated by readjustment of compartment sizes. Efficiency losses following richness losses will have no lasting effects on process rates under flow equilibrium conditions.

List of Hypotheses (4)

Effect-type	Richness effect expected No	 Yes	 Scale-dependent
Reduced variance in space and time (due to levelling-out of fluctuations)	**Motile organisms**	**Sessile organisms**	**Space (Time)**
Intensified habitat exploitation (due to complementary resource utilisation)	**Species-rich communities**	**Species-poor communities**	**Transitory in time**
Higher average activity (due to complementary tolerances)	**Organisms with differing tolerances for reproduction and activity**	**Organisms without decoupling of reproduction and activity**	
Improved ecosystem function (due to synergy of activities)	**Processes that underlie flow-equilibrium**	**Non-equilibrium processes**	**Transitory in time**

Expected richness effects

Weak	**Strong**
Motile organisms Organisms with differing tolerances for reproduction and activity	Sessile organisms Organisms without decoupling of reproduction and activity
Higher animals ***(Protozoans ?)***	**Bacteria, Fungi** **Plants**
Species-rich communities	**Species-poor communities**
Processes that underlie flow-equilibrium	Non-equilibrium processes
Litter decomposition	**Primary production** **Nutrient losses**
	Large areas ***Transitory in time***

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Interim conclusion

In an important variety of cases, diversity probably exerts only weak effects on ecosystem function.

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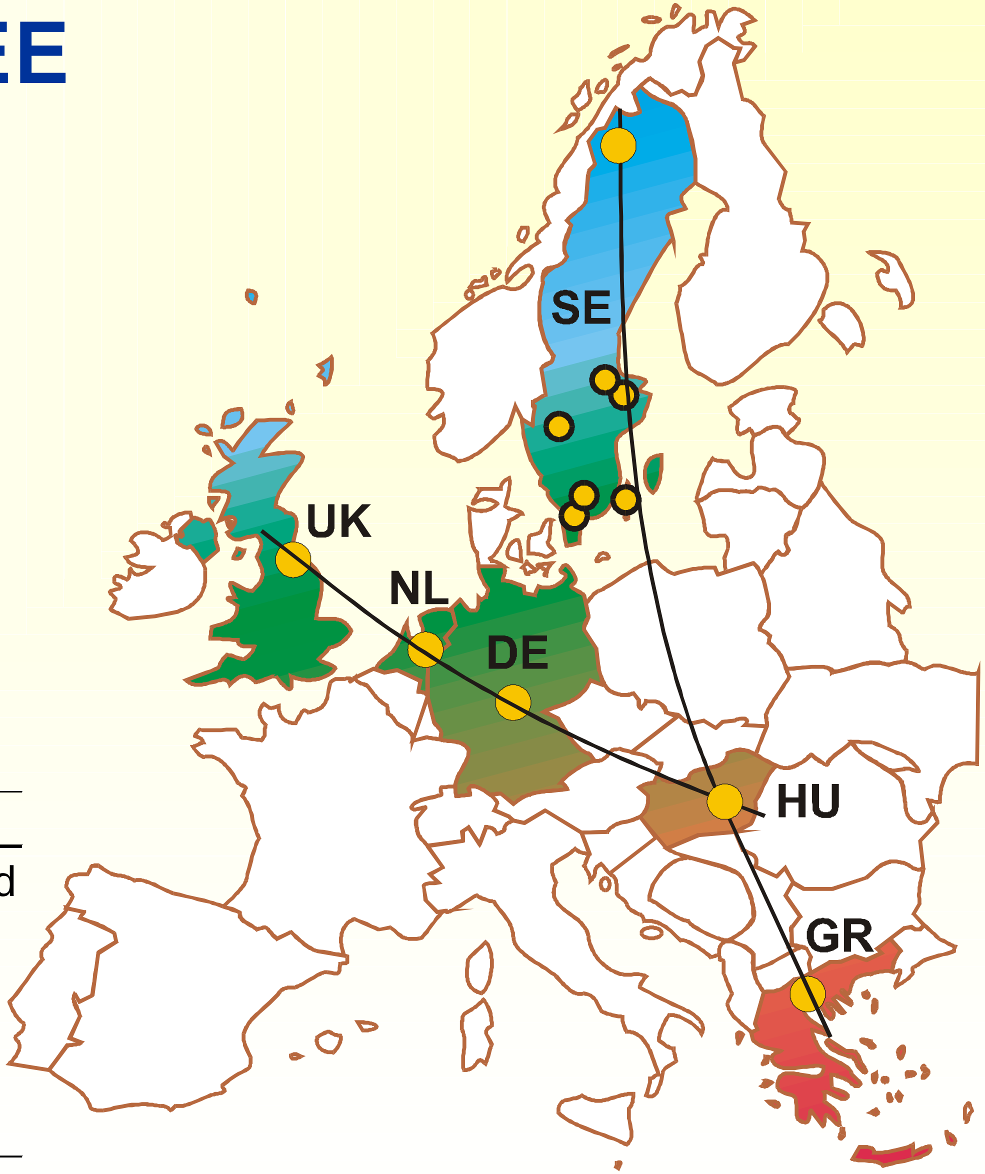
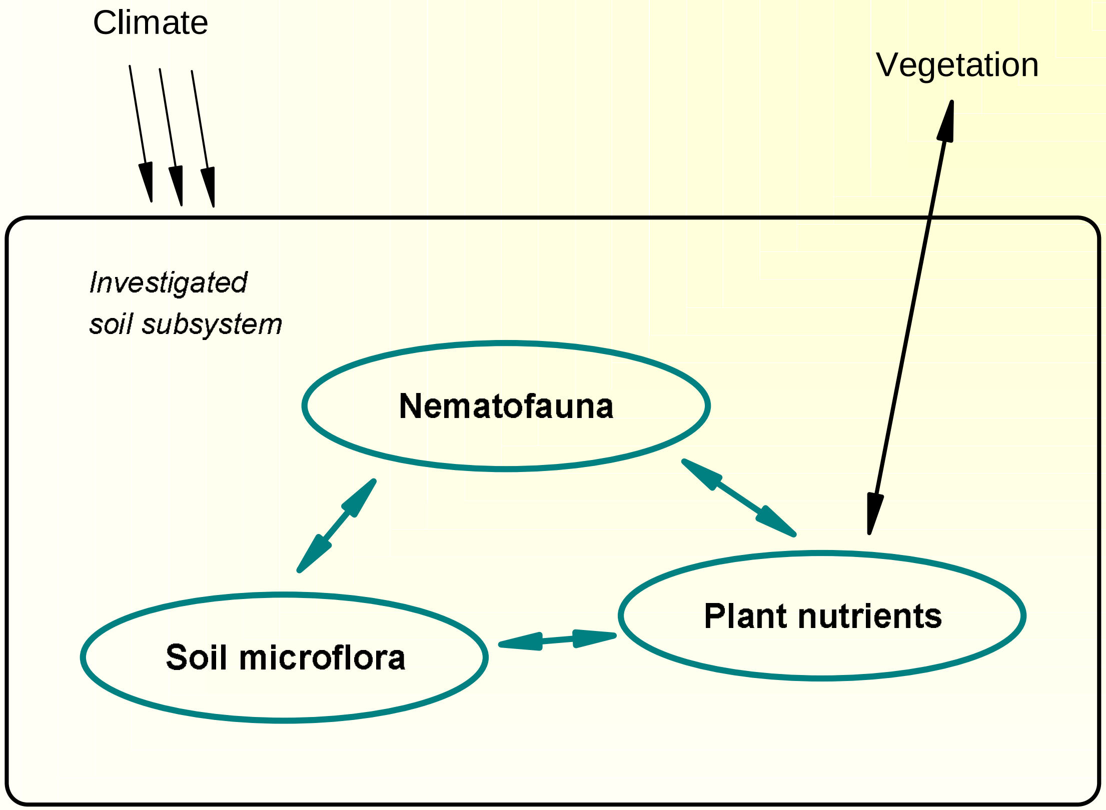


Diversity Effects in Grassland Ecosystems of Europe

Grassland type

DE: Seminatural temperate grassland
SE: Northern tundra
UK: Atlantic heath
NL: Wet grassland
GR: Mediterranean garigue
HU: East European steppe

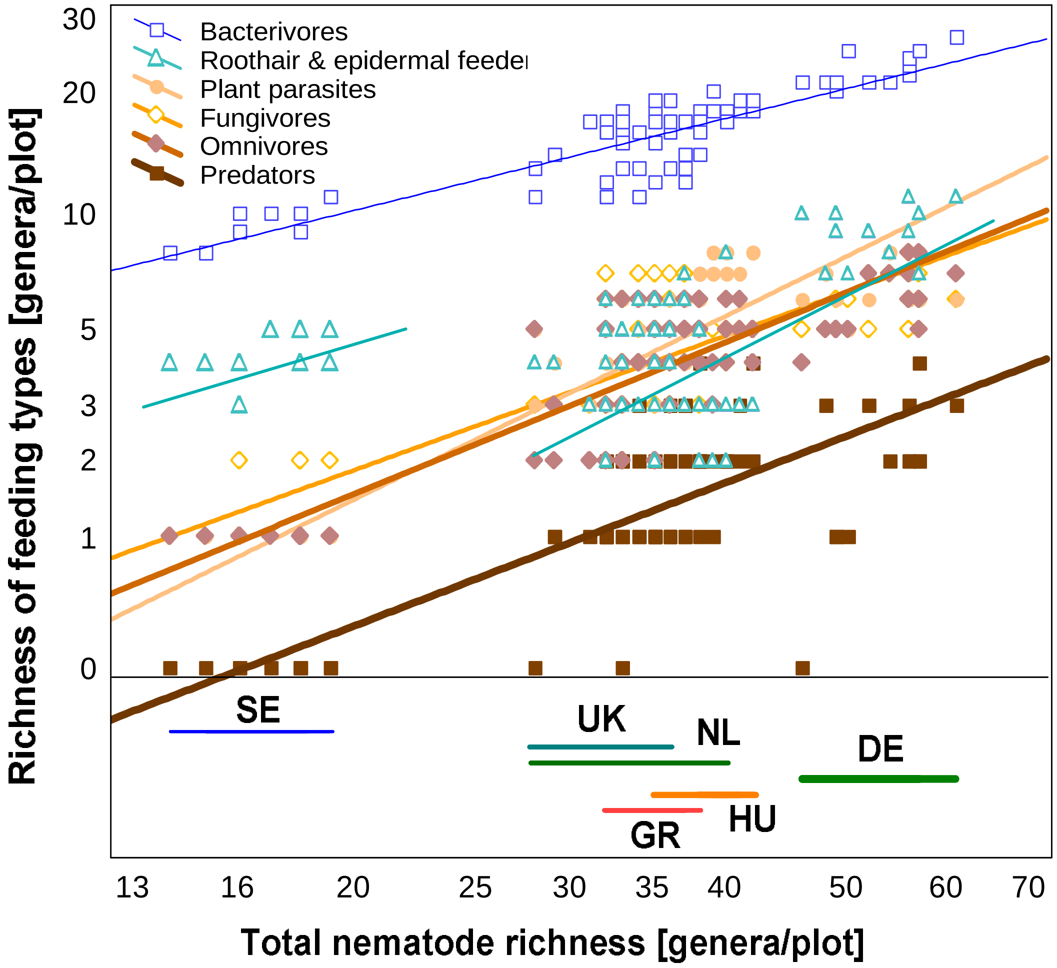
Investigated subsystem of the soil system



Hypothesis:

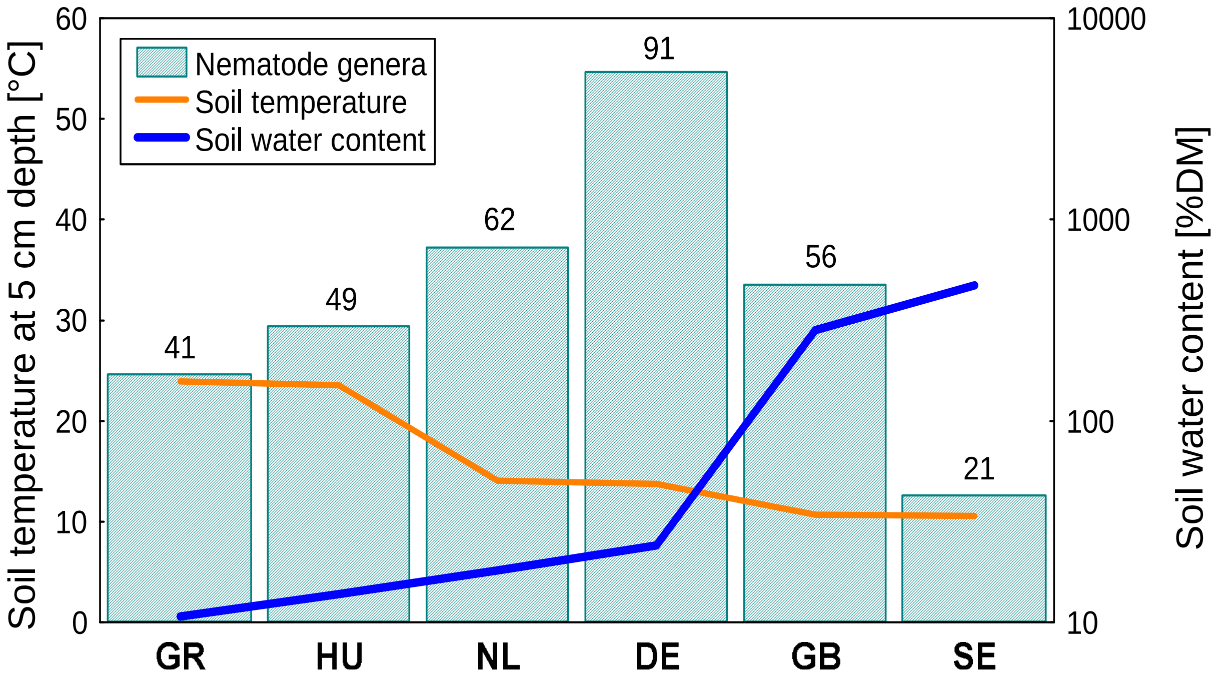
Higher nematode richness leads to (1) higher average levels, (2) reduced spatiotemporal variation, and (3) extended microclimatic niche of (a) nematode abundance and activity, (b) microbial abundance and activity, and (c) soil nitrogen pools.

Observed diversity patterns



a) Relation of nematode richness among nematode feeding types

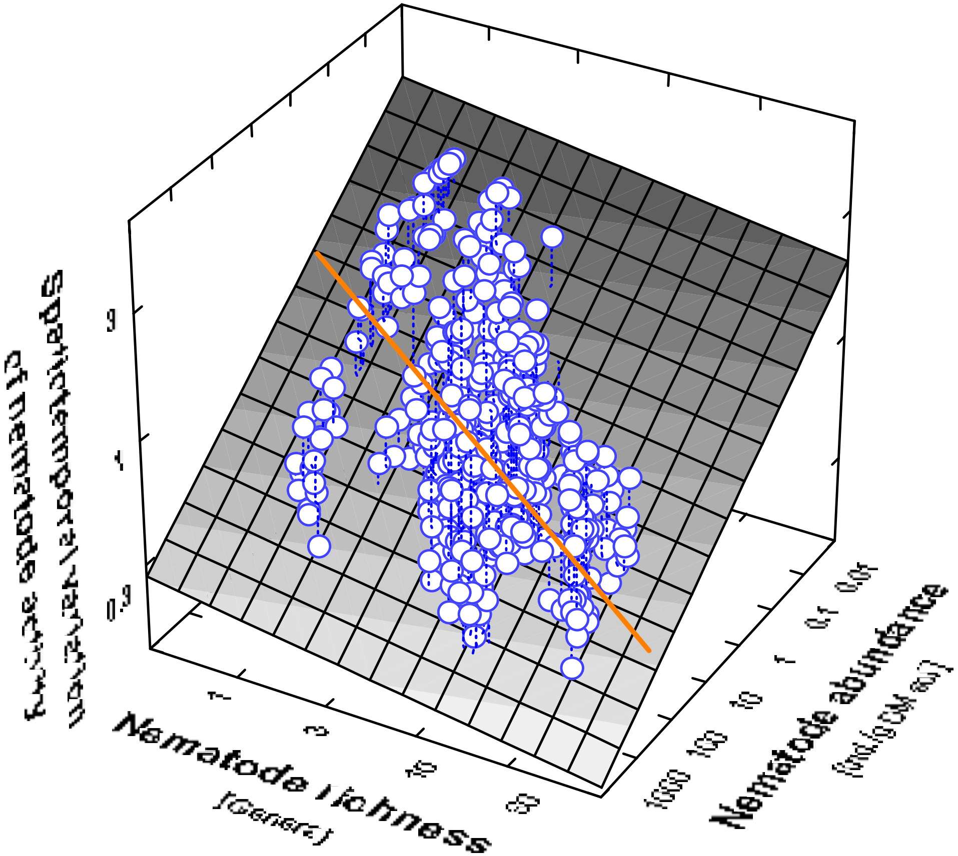
Observed diversity patterns (2)



b) Response of nematode richness to climate

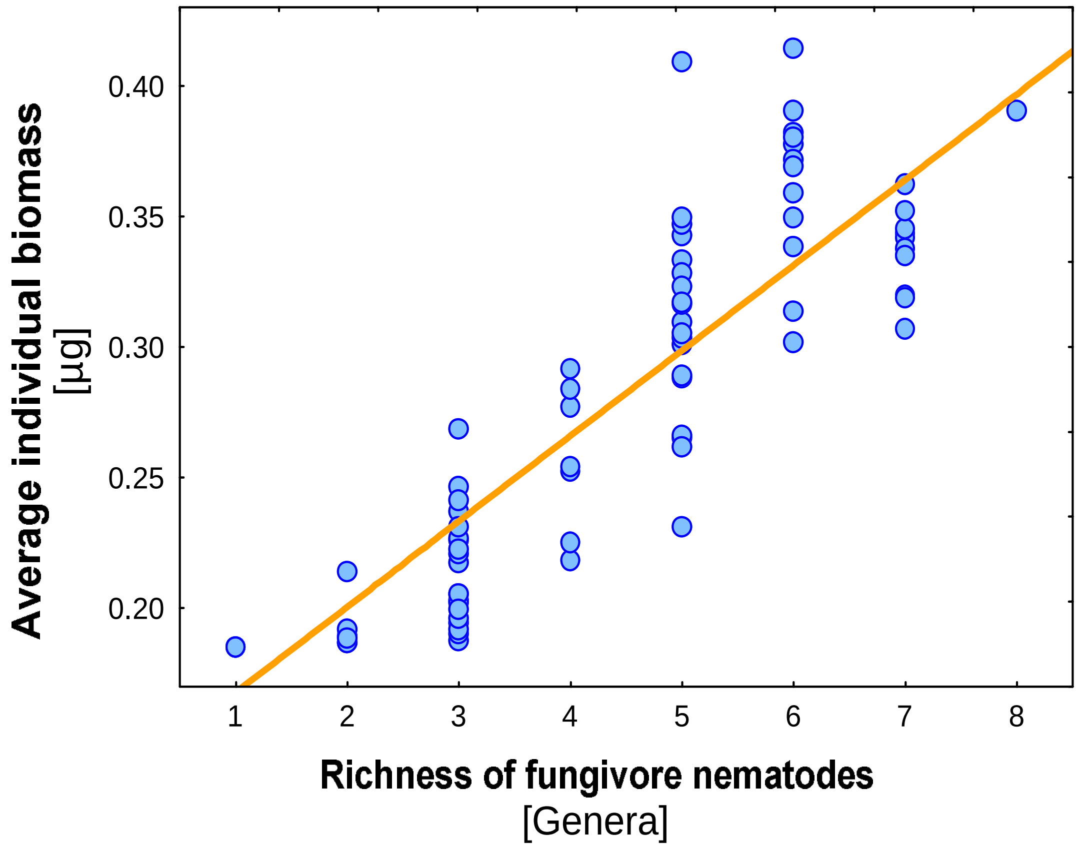
Conclusion: Richness varied considerably, and variation was clearly structured.

Cross-correlations



a) Crosscorelation of abundance and richness of total nematodes

Cross-correlations (2)



b) Cross-correlation of richness and body size in fungivorous nematodes

<u>**Conclusion:**</u> **Cross-correlations (hidden treatments) can feign richness effects, where there are none. Cross-correlations must be carefully eliminated.**

Effects of nematode richness

Target parameter	Average level	Spatio-temporal variation	Tempera-ture niche	Humidity niche	Result counts
Nematode abundance					
Total nematodes	*-3%*	**s.r.**	*-3%*	*-0.5%*	**8 pro**
Bacterivores	*-3%*	*-4%*	n.s.	n.s.	**8 contra**
Fungivores	n.s.	n.s.	n.s.	**+2%**	1 replaced
Roothair & epidermal f.	**+13%**	n.s.	*-3%*	*-2%*	**p = 0.000**
Plant parasites	**+6%**	**+5%**	**+8%**	**+17%**	
Predators	**+13%**	**+25%**	n.s.	n.s.	
Omnivores	n.s.	n.s.	*-5%*	n.s.	
Nematode respiration					
Total nematodes	n.s.	*-13%*	*-3%*	n.s.	**3 pro**
Bacterivores	**s.r.**	n.s.	n.s.	n.s.	**3 contra**
Fungivores	**s.r.**	n.s.	n.s.	**+5%**	5 replaced
Roothair & epidermal f.	**s.r.**	n.s.	*-4%*	n.s.	**p = 0.002**
Plant parasites	n.s.	**+12%**	**+11%**	**s.r.**	
Predators	**s.r.**	n.s.	n.s.	n.s.	
Omnivores	n.s.	n.s.	n.s.	n.s.	
Microbial parameters					
Microbial biomass	n.s.	n.s.	n.s.	n.s.	**2 pro**
Ergosterol	**+13%**	n.s.	n.s.	n.s.	**0 contra**
Soil respiration	n.s.	**+8%**	n.s.	n.s.	1 replaced
Biolog	**s.r.**	n.s.	n.s.	n.s.	p = 0.189
Nitrogen pools					
NO3	n.s.	n.s.	n.s.	n.s.	**0 pro**
NH4	n.s.	n.s.	n.s.	n.s.	**0 contra**
Norganic	n.s.	n.s.	n.s.	n.s.	0 replaced
					p=0.540

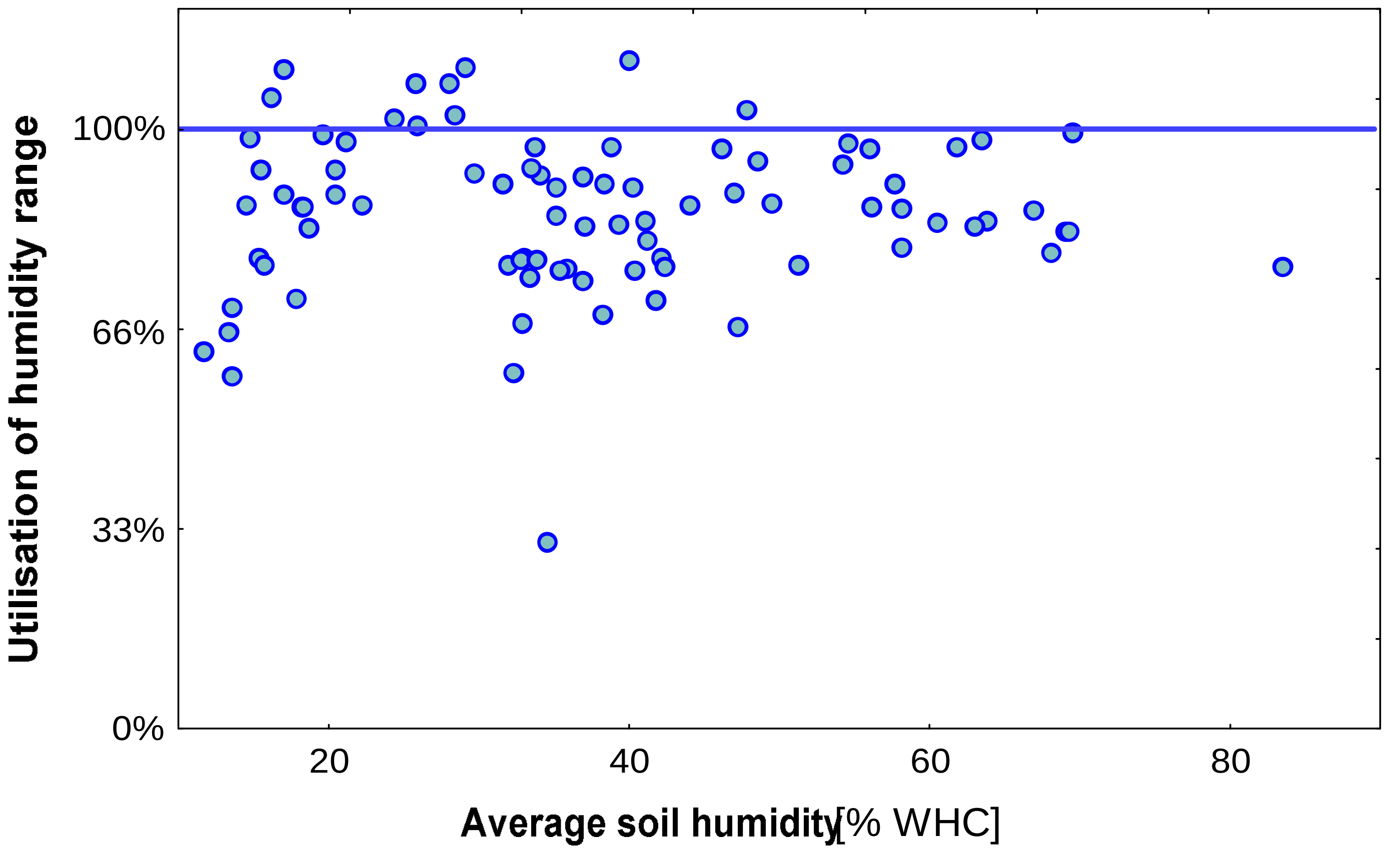
(Multivariate
log-linear
regressions)

Conclusions:

Of the 84 regressions tested, 13 confirmed the hypothesis, while 11 significantly contradicted the hypothesis. Abundance of plant parasitic nematodes was the only among 21 parameters to fully match the hypothesis.

Habitat utilisation

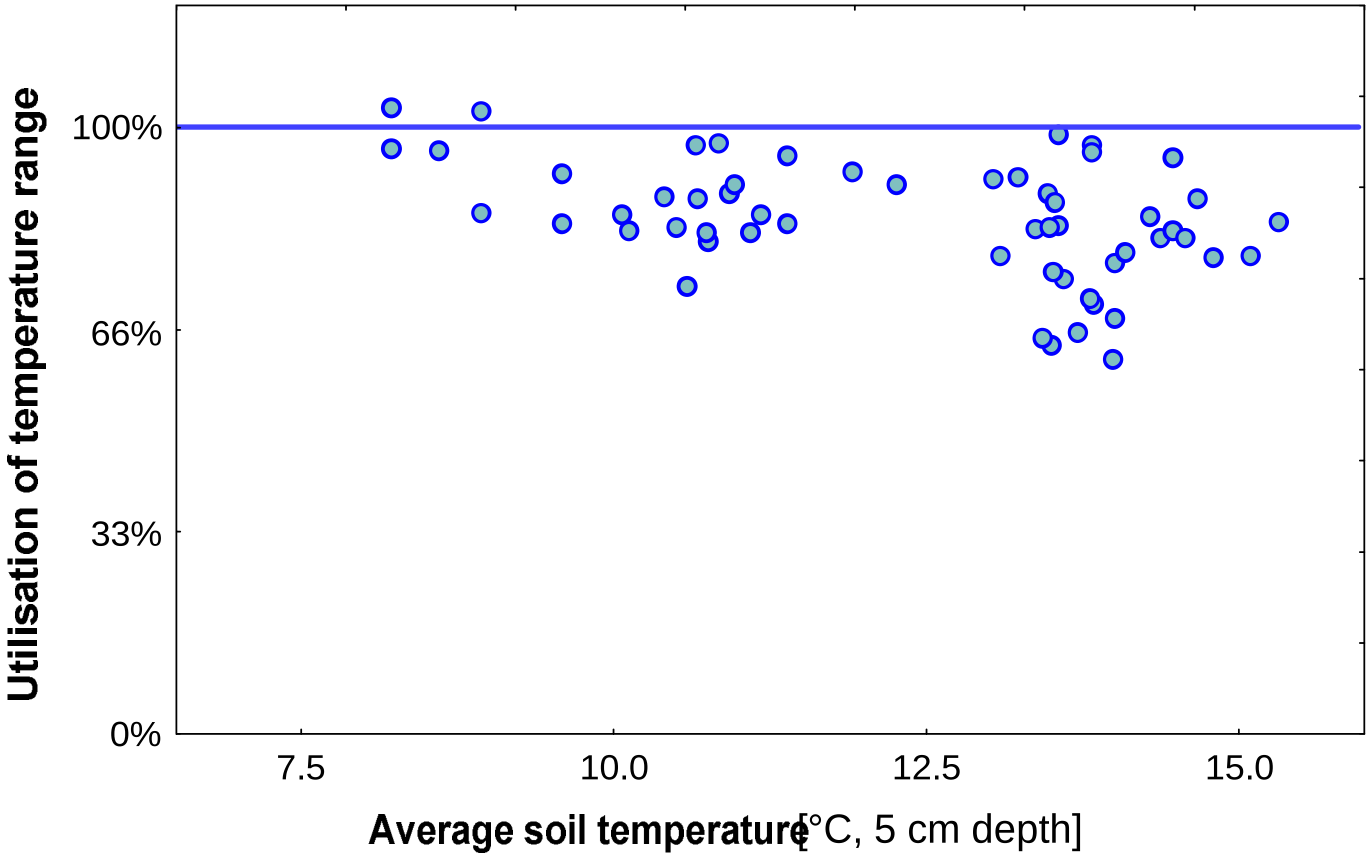
Climate niche of nematode respiration



a) Humidity niche of the total nematofauna

Habitat utilisation (2)

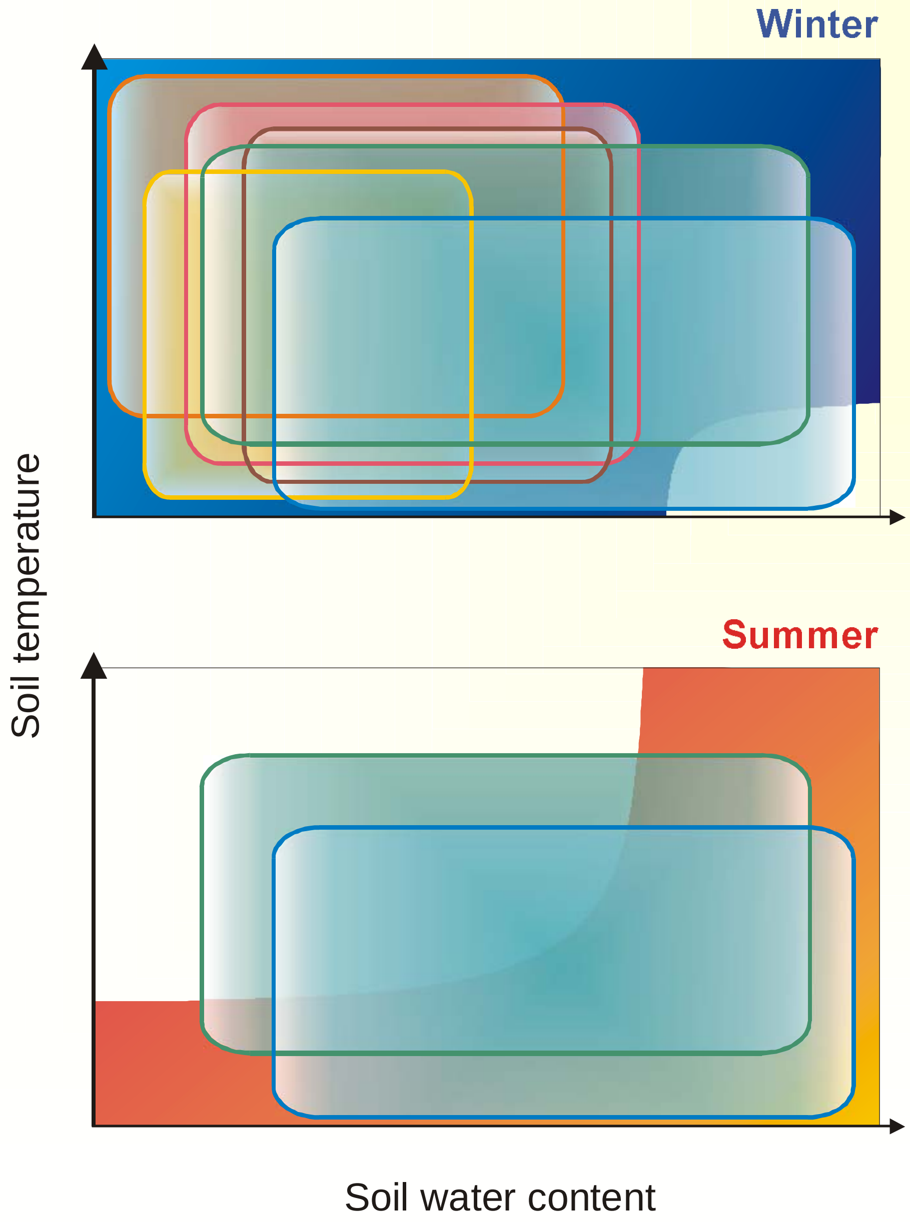
Climate niche of nematode respiration



b) Temperature niche of the total nematofauna

Conclusion: **Summer conditions did not substantially restrict nematode activity**

Decoupling of persistence and activity



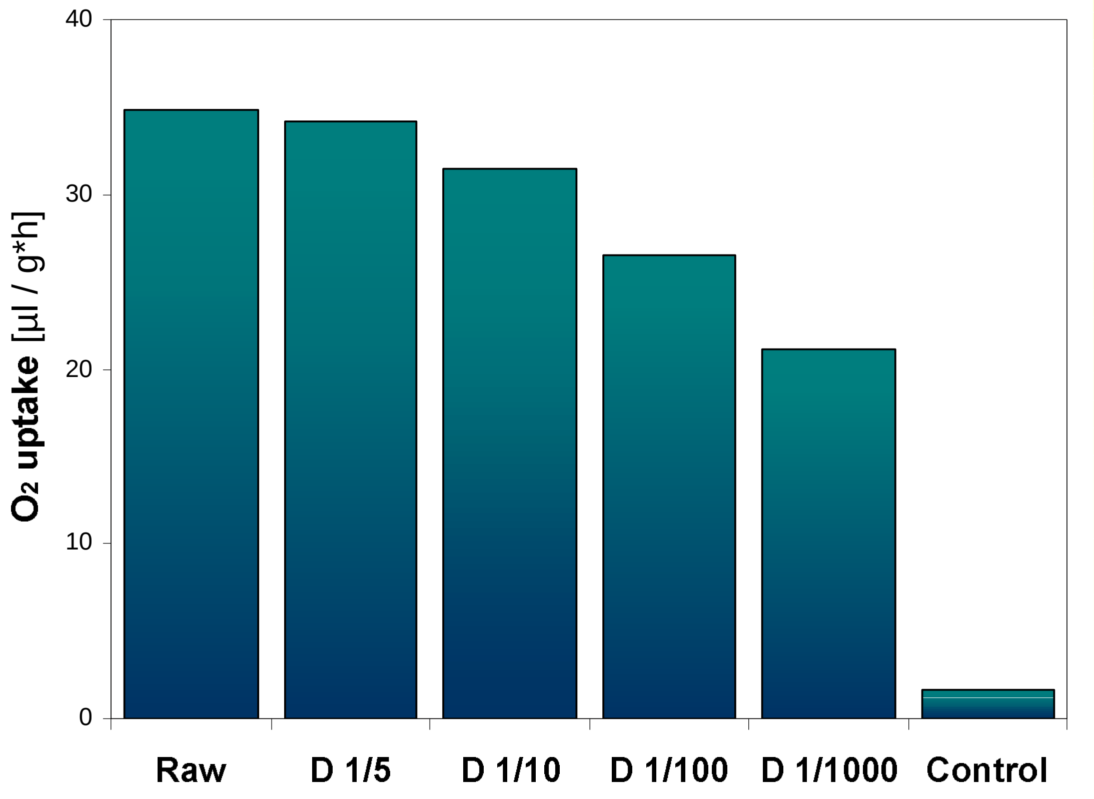
Conclusion:

Once nematode species survived the selective conditions during winter, their activity was not restricted by the moderate conditions in summer.

Therefore, richness did not increase community activity in summer.

Effect of microbial diversity

Salonius 1981. Soil suspensions were diluted in sterile water to produce soil microbial populations of reduced species diversity. Diluted populations (bacteria and fungi) were inoculated into sterile soil and incubated for 5 months at 20°C to allow them to fully colonise the soil.



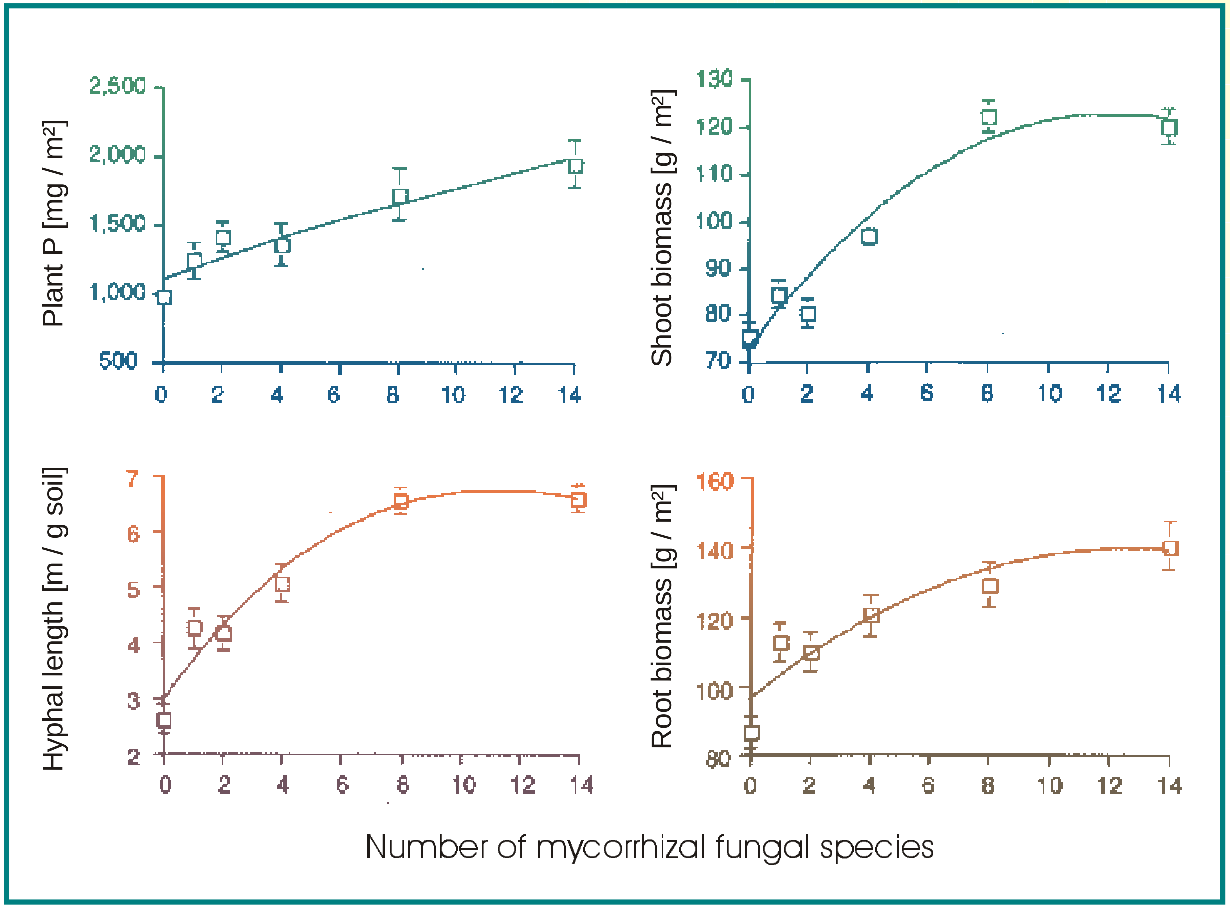
(after Salonius 1981, Fig. 3, day 8)

Conclusion:

Activity of the soil microbial community (O2 uptake) decreased consistently with decreasing community richness.

Effects of mycorrhizal diversity

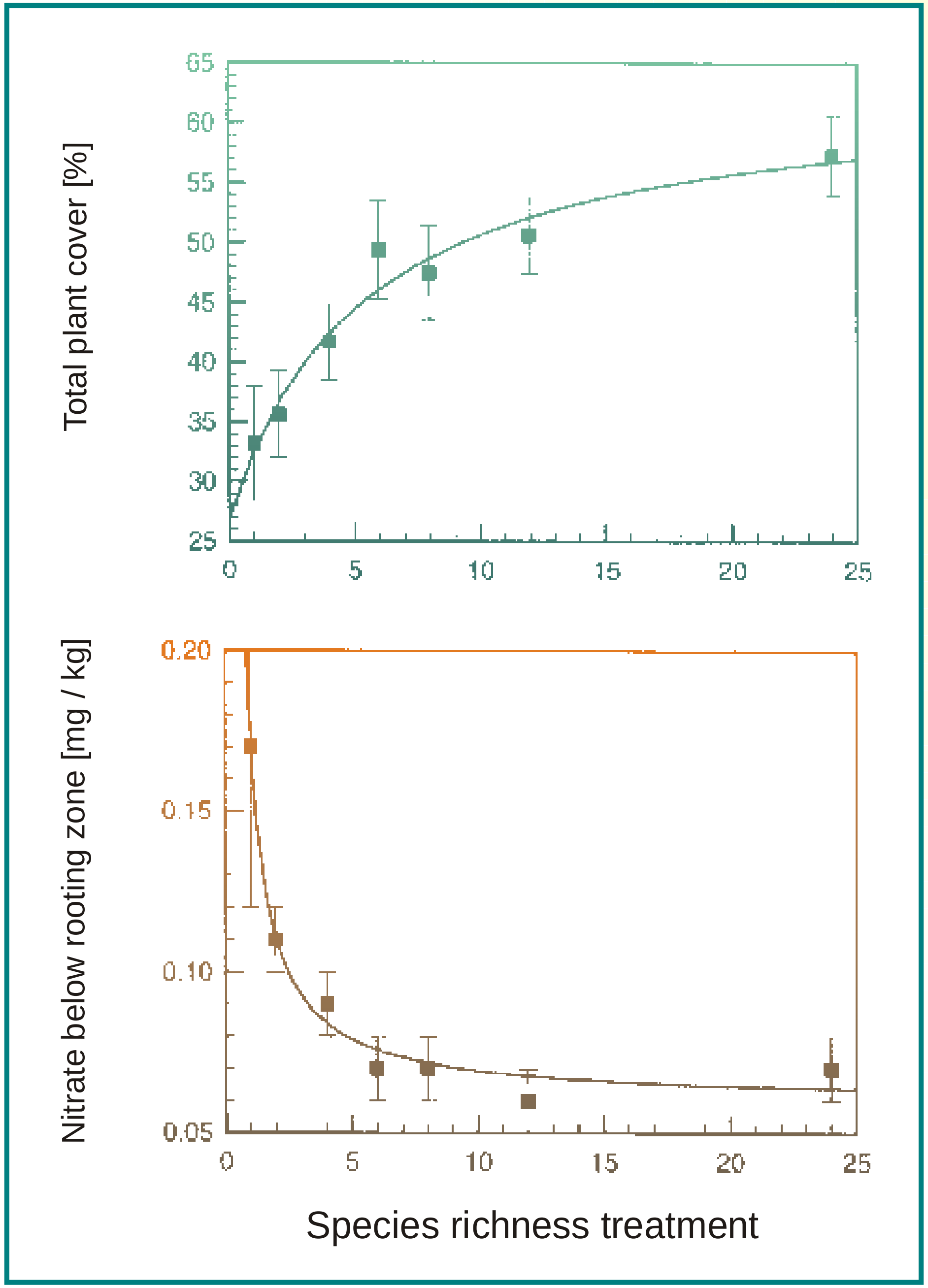
van der Heijden et al. 1998. 70 field macrocosms with sterilised soil received a seed rain simulating North American old-field ecosystems, and were incubated with arbuscular mycorrhizal fungi from a pool of 23 species. Plants were harvested after one growing season.



Conclusion:

Higher mycorrhizal diversity led to increased growth of mycorrhiza and plants.

Effects of plant diversity



Tilman et al. 1996. 147 field plots were planted with different numbers of species from a pool of 24 North American Prairie species. Measurements were made during the second year of growth.

Conclusion:

Higher plant diversity led to higher plant cover and to less leaching of nitrogen.

Empirical evidence

Organisms	Effect of higher diversity on abundance, activity and spatiotemporal variation	Source
Soil animals		
Soil nematodes	Idiosyncratic response of abundance	Ekschmitt et al.
Soil nematodes	Idiosyncratic response of respiration	Ekschmitt et al.
Soil nematodes	Idiosyncratic response of variability	Ekschmitt et al.
Collembola	Idiosyncratic response of soil CO2	Klein et al. (unpubl.)
Summary	***INCONSISTENT***	
Microorganisms		
Soil MO	Increased O2 uptake	Salonius 1981
Mycorrhiza	Increased hyphal length	van der Heijden et al. 1998
Aquatic MO	Increased ecosystem respiration	McGrady-Steed et al. 1997
Aquatic MO	Reduced variability of CO2 flux	McGrady-Steed et al. 1997
Summary	***YES***	
Plants		
Plants	Increased plant cover	Tilman et al. 1996
Plants	Increased biomass	Tilman et al. 1997
Plants	Increased biomass	Kutiel and Danin 1987
Plants	Increased above ground biomass	Hooper and Vitousek 1997
Plants	Reduced variability of biomass	Tilman 1996
Summary	***YES***	

Empirical evidence (2)

Diversity of	Effect on decomposition	Source
Soil nematodes	Increased active fungal biomass	Ekschmitt et al.
Soil nematodes	No response of soil respiration	Ekschmitt et al.
Soil nematodes	No response of bacterial substrate utilisation	Ekschmitt et al.
Litter	No response of decomposition rates	Blair et al. 1990
Litter	No response of decomposition rates	Rustad 1994
Litter	Idiosyncratic response of decomposition	Chapman et al. 1988
Litter	Idiosyncratic response of decomposition	Fyles and Fyles 1994
Plant	Idiosyncratic response of decomposition	Wardle and Nicholson 1996
Litter	Idiosyncratic response of decomposition	Wardle et al. 1997
Litter	Enhanced decomposition rate	Salamanca et al. 1995
Aquatic MO	Enhanced decomposition rate	McGrady-Steed et al. 1997
Summary	***RARE***	

	Effect on nutrient losses	
Plants	Reduced cation loss	Ewel et al. 1991
Plants	Reduced nitrogen loss	Tilman et al. 1996
Summary	***(YES)***	

Conclusion: **Empirical evidence largely supports the predictions derived from the present comparison of theories.**

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DG XII, TERI, ENV4-CT95-0029

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