Spatial isolation increases diversity of complex bacterial community

Jennifer Carson[A], Vanesa González[A], Daniel Murphy[A] and Deirdre B. Gleeson[A]

[A]Soil Biology Group, School of Earth & Environment, Faculty of Natural & Agricultural Science, University of Western Australia, Perth, WA, Australia, Email jennifer.carson@uwa.edu.au

Abstract

One of soil ecology's most intriguing puzzles is how so many different bacterial species can coexist in small volumes of soil. This study tested the theory of spatial isolation which proposes that in unsaturated soils with high clay content, bacterial diversity is greater because fragmented aqueous habitats and thin water films spatially isolate bacterial communities from each other. The texture of a sandy soil was altered without altering chemical properties by adding 0 or 10% silt- and clay-sized particles. Both textures were incubated at several water contents. The effect on the active bacterial communities was measured using terminal restriction fragment length polymorphism (TRFLP) of bacterial 16S rRNA. Bacterial diversity was higher at the lowest soil water content ($P < 0.012$), but was not affected by texture ($P > 0.553$). Bacterial community structure in soil was affected by water content and texture ($P < 0.001$). In ordination plots, bacterial communities were separated into those incubated at water contents of < or >56% water-filled pore space and those in the two textures. This study supports the hypothesis that water content affects the spatial isolation of complex bacterial communities in soil. Given that most soils are unsaturated, these findings suggest that spatial isolation may provide a fundamental theory to explain the high diversity of bacteria in soil.

Key Words

Bacterial diversity, soil, spatial isolation, soil ecology, TRFLP.

Introduction

Soil bacteria are among the most diverse groups of organisms on earth (Torsvik *et al.* 2002) and 4 x 10^6 taxa may coexist in a single tonne of soil (Curtis *et al.* 2002). One of soil ecology's most intriguing puzzles is how so many different bacterial species can coexist when competition theory predicts that less competitive species would decline and eventually disappear (Tilman 1982; Deschesne *et al.* 2007). Tiedje *et al.* (2001) proposed the theory of spatial isolation which predicts that in unsaturated soils with high clay content, fragmented aqueous habitats and thin, tortuous water films spatially isolate bacterial communities from each other (Tiedje *et al.* 2001). These conditions may reduce competition and allow bacterial species to coexist. Low water contents and slow rates of diffusion have been shown to favour the coexistence of two bacterial species competing for a single substrate in modelling studies (Long and Or 2005; Dens and Van Impe 2001) and laboratory studies in agar (Dechesne *et al.* 2008) and artificial soils (Treves *et al.* 2004). There is relatively little evidence about the effect of soil texture on bacterial diversity, but it has been shown to be higher in the clay fraction of soil than the sand fraction (Ranjard *et al.* 2000; Sessitsch *et al.* 2001; Torsvik and Ovreas 2002). The theory of spatial isolation has not been experimentally tested in a field soil with a complex bacterial community and a variety of naturally occurring substrates. In this study we tested hypothesis that the spatial isolation contributes to the high diversity of bacterial communities in soil.

Methods

The texture of a quartz-based sandy soil was altered by adding 0 or 10% silt-and clay-sized particles of quartz (Rocla Quarry Products, Australia). Each texture ('sand' and 'silt+clay') was incubated for 7 d at water potentials between -15 cm (high water content) and -55 cm (low water content). The effect of water potential and texture on the diversity and structure of bacterial communities was measured using TRFLP of bacterial 16S rRNA.

Results

Water potential and texture significantly affected bacterial community structure ($P < 0.001$). In ordination plots, bacterial communities clustered into four groups depending on whether they were incubated in sand or silt+clay and whether the water-filled pore space of soil was < 56% or > 56% (Fig. 1). Most pairwise comparisons between bacterial communities in different clusters were significantly different ($P < 0.05$). Water potential significantly affected the richness (S, eH') and diversity (H', 1/D) of bacterial communities ($P < 0.012$) but texture did not ($P > 0.553$). In both textures, the richness and diversity of bacterial communities was higher at water-filled pore space < 56% than at water-filled pore space > 56% (Table 1).

Table 1. The richness, evenness & diversity of bacterial RNA-TRFLP profiles incubated in 0% silt+clay (sand) and 10% silt+clay (Silt+clay) at a range of water potentials. Least significant difference (lsd, $P < 0.05$) was determined by two-way analysis of variance. Mean (±standard error), TRFLP profiles n =4.

Texture	Water potential	Bacterial TRFLP profiles				
		S	eH'	H'	1/D	J'
Sand	15	105	58	4.05	43	0.871
	20	102	56	4.03	40	0.870
	25	116	73	4.28	54	0.901
	30	115	66	4.18	47	0.882
	40	112	66	4.19	47	0.888
	55	119	71	4.26	50	0.891
Silt+clay	15	101	60	4.09	46	0.886
	25	100	56	4.03	42	0.875
	35	107	65	4.17	50	0.892
	40	111	70	4.24	54	0.901
	45	111	71	4.25	55	0.903
	55	118	70	4.24	50	0.890
lsd		11	14	0.23	13	0.036

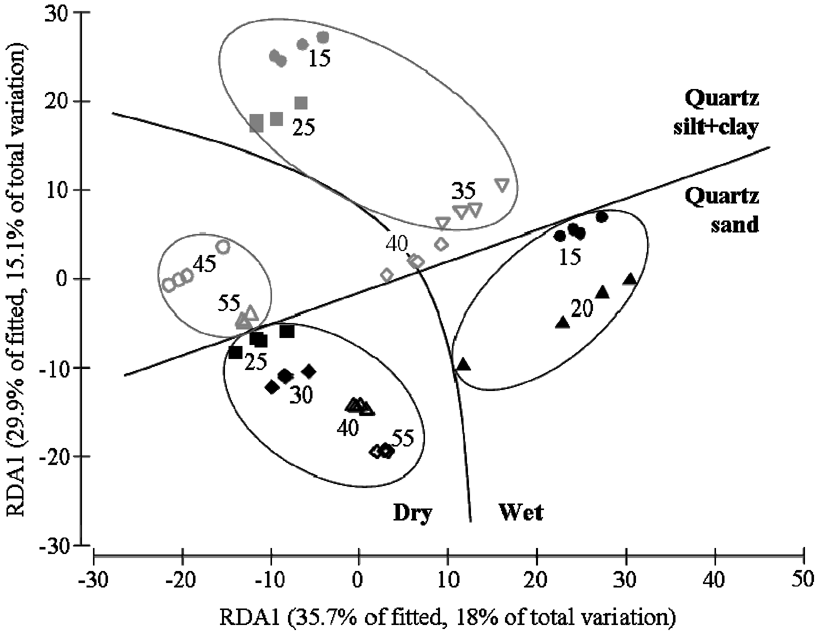

Figure 1. Distance-based redundancy analysis (dbRDA) of bacterial communities incubated at water potentials shown (-cm) in either sand (black symbols) or silt+clay (grey symbols, separated by straight line). Circles surround bacterial communities that did not differ from each other ($P > 0.05$). The curved line separates bacterial communities incubated in 'Wet' and 'Dry' soils (water-filled pore space > or <56%). All pairwise comparisons across the curved line were significantly different ($P < 0.05$, except silt+clay -15 cm and -55 cm which did not differ). Soil variables used to generate the dbRDA were: water-filled pore space (% total pore volume), silt+clay content (% wt/wt), largest water-filled pore and the volume of water in pore size classes 68-77, 77-88, 88-102, 102-122, 122-153 and 153-204 µm. The figures in brackets indicate the percentage of the fitted and total variation explained by each axis.

Conclusion

The findings of this study support the hypothesis that bacterial diversity in soil increases as water content decreases. Previous studies testing the theory of spatial isolation have used only two bacterial species competing for a single substrate and were either modelling studies (Long and Or 2005; Dens and Van Impe 2001) or did not use field soils (Dechesne *et al.* 2008; Treves *et al.* 2004). In contrast, the present study used a molecular technique (RNA-TRFLP) to show that decreasing the water content of soil increased the diversity and altered the structure of a complex, indigenous bacterial community in a field soil with a variety of naturally occurring substrates. Since field soils are usually unsaturated, the theory of spatial isolation may provide a fundamental principle to explain the high diversity of bacteria in soil (Tiedje *et al.* 2001). Although increasing the silt+clay content was not shown to increase bacterial diversity, it did alter the structure of the bacterial communities. Previous studies showing that silt- and clay-sized particles are associated with bacterial communities with different structure and greater diversity compared to sand-sized particles (Ranjard *et al.* 2000, Sessitsch *et al.* 2001, Torsvik and Ovreas, 2002) have not taken into account their different mineral type and composition, which is known to affect bacterial community structure (Carson *et al.* 2009). In this study, because soil texture was altered by adding silt- and clay-sized particles of quartz to a quartz based sand, it was possible to attribute the effect of texture on bacterial communities to the altered physical conditions in soil.

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