

Competition hierarchy, transitivity and additivity: investigating the effect of fertilisation on plant–plant interactions using three common bryophytes

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Received: 1 June 2006 / Accepted: 2 November 2006 / Published online: 27 December 2006
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Abstract The way competition structures plant communities has been investigated intensely over many decades. Dominance structures due to competitive hierarchies, with consequences for species richness, have not received as much experimental attention, since their manipulation is a large logistic undertaking. Here the data from a model system based on bryophytes are presented to investigate competition structure in a three-species system. Grown in monocultures, pairwise and three-species mixtures under no and high nitrogen supply, the three moss species responded strongly to treatment conditions. One of them suffered from nitrogen fertilisation and hence performed better in mixtures, where the dominant species provided physical shelter from apparently toxic nitrogen spray. Accordingly, no linear competitive hierarchy emerged and qualitative transitivity remains restricted to the unfertilised treatments. Facilitation also affected other properties of the competition structure. The reciprocity of competition effects could not be observed. Moreover, the performances in three-species mixtures were not well predictable from the knowledge of

monocultures and pairwise mixtures because competitive effects were not additive. This had implications for community stability at equilibrium: all two-species systems were stable, both fertilised and unfertilised, while the three-species system was only stable when fertilised. This stability under fertilisation has probably to do with the facilitative effect of the two dominant species on the third. In this experiment, little support for commonly held ideas was found about the way competition in plant communities is structured. On the other hand, this study shows that moss communities are ideal model systems to test predictions of theoretical models concerning properties and consequences of competition in plant communities.

Keywords Bryophytes · Community matrix · Competition · Facilitation · Lotka–Volterra · Stability · Transitivity

Introduction

In plant ecology, competition has often been stated as the main cause of species exclusion from communities (but see Gleason 1926; Hubbell 2001; Keddy 1989). Competition has been shown to influence plant growth (e.g. Tilman and Wedin 1991; Wedin and Tilman 1993), vegetation composition (e.g. Fowler 1981; Goldberg

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1994; Goldberg et al. 1995) and spatial associations in communities (e.g. Tirado and Pugnaire 2005). Therefore understanding competition is important to comprehend the way communities are structured and how species coexistence is brought about. Unravelling the way competition structures communities has been attempted mainly by theoretical models, which predict certain characteristics of competitive relationships between coexisting species. Among them are competitive hierarchies (Goldberg and Landa 1991; Keddy 1989) (related to this: transitivity of competition), reciprocity (Freckleton and Watkinson 2001b) and additivity of competitive effects (Dormann and Roxburgh 2005). For terrestrial plant communities, for example, there is no documented case of intransitive hierarchies (Keddy and Shipley 1989; Shipley 1993), i.e. in all cases, if A is dominant over B and B is dominant over C then A is also dominant over C. This need not be the case in other systems, such as bryozoa or algae (Buss 1986), and the consequences of intransitivity for coexistence have been predicted to be dramatic (Frean and Abraham 2001). More recently, Freckleton and Watkinson (2001b) have introduced an even stronger definition of *quantitative* transitivity (see methods below). They also investigated an additional potential feature of competitive interactions, namely reciprocity, i.e. the idea that the stronger the effect of species A is on B, the weaker is B's effect on A.

Another line of recent research has tested if pairwise interactions give all the information needed to model entire communities, as is implicitly assumed in most coexistence models. Species interactions are usually summarised in a $n \times n$ community matrix S (Case 2000; Keddy 1989; Levins 1968), where matrix element s_{ij} represents the *per capita* effects of species j on species i . The analysis of this community matrix, e.g. with respect to stability at equilibrium (Case 2000), implicitly assumes that interaction effects of different species add to the total effect (Case 2000; Case and Bender 1981; Wootton 1994a, b). The analysis of multi-species competition experiments so far has rejected the idea of additivity of competitive effects for plant communities (Dormann and Roxburgh 2005).

Understanding which features competition-organised communities have is essential to predicting their potential for coexistence (Keddy and Shipley 1989). For example Roxburgh and Wilson (2000) showed with data from an experimental lawn community, that transitivity makes communities in mathematical models more likely to be stable. Hence, any progress made in unravelling common features of competitive structures is a step towards the possibility to more realistic coexistence models. Evaluation of how external perturbations impact competitive structure may provide insight into which processes affect the susceptibility of plant communities to changes in the environment.

Rees et al. (1996, 2001) as well as others (e.g. Aarssen 1988; Freckleton and Watkinson 2001a) have attempted to extract information on competition intensity from long-term field observation. While necessarily of a correlative nature, these studies clearly point at variation in competition intensity as a key driver of community composition. On the other hand studying the effect of competition on community composition experimentally is a logistic challenge (e.g. Roxburgh and Wilson 2000). Experimental studies are nonetheless imperative to test specific theoretical predictions and to validate mechanistic models (Diamond 1986).

The report on a study in a model system designed to (1) quantify the strength of plant–plant interactions, (2) investigate the degree of transitivity in competitive hierarchies, (3) examine the predictability of species performance in multi-species mixtures from pairwise interactions, and (4) assess the effects of nitrogen fertilisation on these parameters. Bryophytes have been shown previously to be excellent systems for addressing questions of coexistence and competition (Mulder et al. 2001; Rixen and Mulder 2005), because they are small enough for high levels of replication in the greenhouse (Zamfir and Goldberg 2000), but still large enough to avoid using time-consuming microscope work (as in the case of algae). Moreover, they may serve as representative also for vascular communities (Steel et al. 2004; Wilson et al. 1995). Homogeneous mixtures and exact initial starting dosage can easily be achieved (see methods).

Methods

Study species

Bryophytes are organisms highly adapted to harsh environmental conditions and disturbances. They can withstand near-complete desiccation, extremely low temperatures, physical fragmentation and years of physiological inactivity (Richardson 1981). As a consequence, bryophytes dominate arctic and alpine tundra, making them an important component of these systems (Archibald 1994). Their robustness makes them an ideal set of organisms to work with experimentally. In this experiment, three common bryophytes were used: *Calliergonella cuspidata*, *Plagiomnium undulatum* and *Rhytidiadelphus squarrosus* (nomenclature follows Frahm and Frey 1992). All three are described as nitrophytic by Dierßen (2001). *Calliergonella cuspidata* and *R. squarrosus* share a preference for open, grassy habitats, while *P. undulatum* occurs more commonly in woodland, but also in damp grassland. The three species may co-occur (e.g. in the botanic garden where the experiment was carried out), but they differ in growth form. *Rhytidiadelphus squarrosus* grows upright in dense, monospecific stands. *Plagiomnium undulatum* occurs in loose mats formed by lateral spreading. *Calliergonella cuspidata* has a very variable morphology. It is a creeping plant, able to weave itself into stands of other species (e.g. *P. undulatum*), but it can also form monospecific stands under optimal growing conditions.

These three species were selected because their commonness and local dominance suggested vigorous growth and competitive strength. Data from previous studies give contradicting evidence to competitive effects of mosses: while *C. cuspidata* and *R. squarrosus* share a high competitive ability (Kooijman and Bakker 1995; van der Hoeven et al. 1998) other feathermosses showed no competitive effect (McAlister 1995; Mulligan and Gignac 2002). Mosses were collected in the botanical garden of the University of Leipzig (*P. undulatum* and *R. squarrosus*) and from an inner-city brownsite (*C. cuspidata*).

Experimental design

The experiment consisted of factorial competition × fertilisation manipulations: two levels of ammonium nitrate (0 and 5 g m⁻² a⁻¹) were combined with seven competition treatments (three monocultures, all three pairwise mixtures and the three-species mixture). In a pilot study, all species were subjected to four different levels of nitrogen fertilisation (0, 1.5, 5 and 15 g m⁻² a⁻¹). Fertilisation affected growth of *C. cuspidata* and *P. undulatum* positively except for the highest level. *Rhytidiadelphus squarrosus* showed a slight decrease in biomass in response to fertilisation. Based on these results, the chosen levels of fertilisation was decided. The competition experiment was replicated five times, yielding 70 trays.

A replacement-series with a constant 50 g fresh moss per m² was employed, which in the case of competition treatments was composed of equal amount from each species (i.e. 25 g each in the pairwise mixture, and 16.7 g each in the three-species mixture). This type of experimental design has been criticised (see Gibson et al. 1999, for review). Since the initial biomass was identical for all species in the mixture, most of these criticisms were of little concern here (particularly size bias: Connolly et al. 2001). The remaining shortcoming of this approach is that its conclusions cannot be extended to any density other than the one chosen in this study (Gibson et al. 1999). The advantage of the replacement series approach is that initial species density was constant across all treatments and hence competition effects cannot be explained by density independent of the competing species. For this reason the substitutive approach is also used in the large biodiversity experiments (e.g. Hector et al. 1999; Roscher et al. 2004; Tilman et al. 1996).

Fifty-gram (fresh weight) moss was blended in 1 l of deionised water with a kitchen blender for approx. 2 min. The resulting “stock solutions” (Rixen and Mulder 2005) were poured directly or after mixing with the other species onto trays of 20 × 30 cm filled with 4 cm of commercial potting soil (“Dachgarten spezial”, pH = 6.2). Each tray received 60 ml (approx. 3.2 g fresh weight) moss stock solution.

All trays were randomly placed on two banks in a greenhouse under plastic sheeting to maintain a high humidity and under constant artificial light. Trays were moved by one position sideways every 2 weeks to reduce the effect of a potential light gradient. Temperature in the greenhouse was set to 25°C, but the automatic shading could not prevent temperatures under the plastic sheets to reach maximum values of 32°C during some sunny days. Trays were watered to saturation three times a week with deionised water. Every 2 weeks trays were fertilised according to treatment by placing a plastic frame over the trays (to shield neighbouring trays) and misting the trays with the fertiliser solution. Unfertilised trays received deionised water instead.

Harvest. To overcome edge effects only the central 15 by 15 cm of each tray were harvested 164 days after the initiation of the experiment. Individuals of each species were harvested by manual picking, washing off attached soil, drying for 12 h at 60°C and weighing to the nearest mg.

Analysis of competition, transitivity and additivity

The substitutive design, which kept species density constant in all treatments, prevents a direct comparison of final biomasses, as they derive from different initial densities (Freckleton and Watkinson 2000). Thus while the design prevents different initial densities from confounding the effects of competition, the final biomass data are not necessarily a good estimate of plant performance. Imagine, for instance, that a monoculture and mixture yield the same final biomass. As the preliminary mixture has only half of the initial biomass, this has to be corrected. Simply multiplying by two ignores the non-linear growth of plants at low densities (e.g. Yoda et al. 1963). Therefore, relative growth rates were calculated (RGR) for each species in each tray as (Hutchings 1997):

$$\text{RGR} = \frac{\log_e \text{ final biomass} - \log_e \text{ initial biomass}}{t_{\text{final}} - t_{\text{initial}}},$$

where t refers to time. It is thereby implicitly assume that growth can be approximated by an

exponential function. For the analysis of competition, transitivity and additivity of competitive effects RGR were calculated as a measure of plant performance.

These data allow a direct comparison of monocultures, two- and three-species mixtures by means of the Relative Neighbour Effect (RNE: Grace 1995; Markham and Chanway 1996; Weigelt and Jolliffe 2003):

$$\text{RNE} = \frac{\text{RGR}_{\text{mix}} - \text{RGR}_{\text{mono}}}{\max(\text{RGR}_{\text{mix}}, \text{RGR}_{\text{mono}})}.$$

Positive RNE values indicate facilitation in mixture, while negative RNE values indicate competition (Callaway et al. 2002).

The RNE of a treatment for all $5^2 = 25$ possible combinations of replicates for the two treatments was calculated (i.e. *mix* and *mono*). For the means of the combinatorial values standard errors were used (standard deviation divided by the square root of the number of replicates, in this case 5) to perform t -tests between fertilised and unfertilised means and to test for significant difference from 0.

Next, the competition coefficients for transitivity along the lines outlined in Freckleton and Watkinson (2001b) was analysed. The competition coefficients was calculated, again based on RGR as:

$$\alpha_{ij} = (\text{RGR}_{i \text{ mono}} - \text{RGR}_{i \text{ mix } ij}) / \text{RGR}_{j \text{ mix } ij}.$$

This is the equilibrium solution for Lotka–Volterra-type competition (Gotelli 1995; Istock 1977, see appendix for details). A_{ij} expresses the effect of B in equivalents of A and is hence the same as ε_{ij} in Freckleton and Watkinson (2001b, see appendix). Transitivity then means, if j reduces the performance of i by some factor α_{ij} , and k reduces j 's performance by a factor α_{jk} , then k should reduce i 's growth by the product $\alpha_{ij} \cdot \alpha_{jk}$. If indeed this product equals the measured effect (i.e. α_{jk}), the competitive hierarchy is *quantitatively* transient (Freckleton and Watkinson 2001b). Competition coefficients was calculated for all combinations of the five replicates for the three treatments (i mono, i mix, j mix; i.e. $5^3 = 125$), and used mean and standard deviation

of the combinatorial samples to test for difference between α_{ij} as measured in the respective treatment, and α'_{ij} as product of $\alpha_{ik} \cdot \alpha_{kj}$. Significant differences indicate imperfect or non-quantitative competitive hierarchies.

To assess the long-term outcome of competition, this experiment was used to parameterise a community matrix (Case 2000; Keddy 1989; Levins 1968; Wilson and Roxburgh 1992). Based on Lotka–Volterra competition equations the community matrix specifies the effects of each species onto each other, based on (absolute) growth rates, carrying capacities (i.e. biomass in monocultures) and competition coefficients. As intermediate step, this approach yields the equilibrium biomass for the mixtures (see Case 2000, for details). Note that the outcome is necessarily an extrapolation, since in no mixture did a species fully exterminate the other.

Finally, the relative growth rate of all species in the three-species mixture based on the competition coefficients in the two-species mixtures was predicted (see Dormann and Roxburgh 2005, for details). For all combinations of the five replicates (i.e. $5^6 = 15625$, see appendix), I fitted the observed RGRs to the prediction model using non-linear regression.

All analyses were carried out using the free software R, version 2.1.0 (R Development Core Team 2004).

Results

In monocultures *P. undulatum* and *C. cuspidata* profited from fertilisation by increasing their biomass by approx. 60%. *Rhizidiadelphus squarrosus*, on the other hand, showed a negative response, with the fertilised trays having only half of the biomass compared to the unfertilised ones (Fig. 1). In pairwise and three-species mixtures, tray biomass was always lower than that of monocultures, even for the mixture of the two nitrogen-responsive species. Due to the substitutive design, biomass results are difficult to compare: in the mixtures the initial biomass was only half of the monocultures, and hence expected final biomass will also be lower. Assuming exponential growth in the investigated time period, the

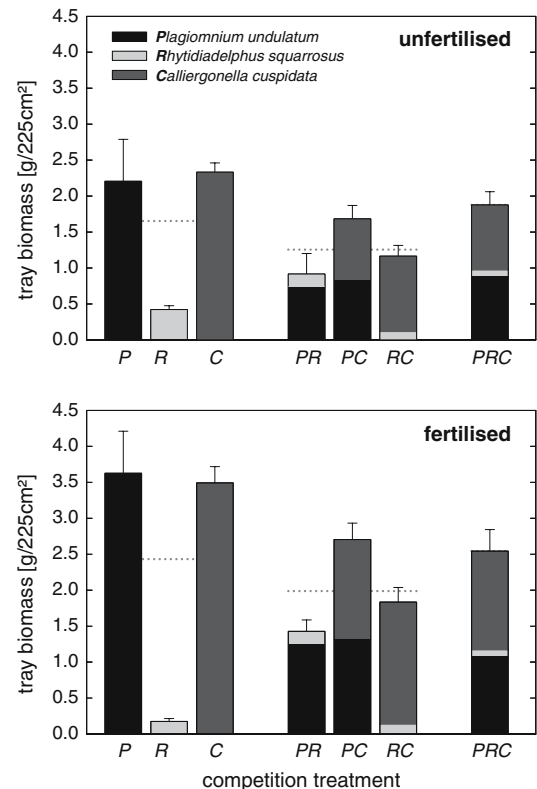


Fig. 1 Tray biomass for the different monocultures and mixtures. Error bars (± 1 SE) indicate variability of total tray biomass. Dotted line represents mean of all monocultures and two-species mixtures, respectively. Single letters under the bars refer to the genus' first letter

focus for the rest of the results will be on the RGR in the different treatments (Table 1).

Calliergonella cuspidata and *P. undulatum* had very similar growth rates in all treatment (Table 1), i.e. both in monocultures and competition treatments for both levels of fertilisation. *Rhizidiadelphus squarrosus* reached only half of its growth rate, in the fertilised monocultures even less. Accordingly, the effects of neighbours on *C. cuspidata* and *P. undulatum* were also very similar (Fig. 2). Both were slightly reduced in growth rate by the other two species, but hardly so in the three-species mixture. For *R. squarrosus* an entirely different picture emerged: it was relatively strongly suppressed by competition in the unfertilised trays, but profited from neighbours in the fertilisation treatments (yielding a positive RNE-value). This was not due to increased growth with neighbours (Table 1), but

Table 1 Relative growth rates (± 1 SE) [mg/day] for the three bryophyte species in monocultures, two- and three-species mixtures

	<i>Plagiomnium undulatum</i>		<i>Rhytidiadelphus squarrosus</i>		<i>Calliergonella cuspidata</i>	
	-N	+N	-N	+N	-N	+N
Mono	24.5 \pm 1.6	28.0 \pm 1.2	15.1 \pm 0.8	8.7 \pm 0.8	25.6 \pm 1.4	28.1 \pm 0.9
PR	21.7 \pm 1.1	25.9 \pm 1.5	13.8 \pm 0.4	13.5 \pm 2.1		
PC	23.4 \pm 1.6	26.2 \pm 1.6			23.6 \pm 1.1	26.5 \pm 1.0
RC			11.3 \pm 1.2	12.3 \pm 2.2	24.8 \pm 1.1	27.8 \pm 1.1
PRC	26.3 \pm 1.1	27.4 \pm 1.1	11.8 \pm 1.8	11.9 \pm 1.2	26.5 \pm 0.8	28.9 \pm 0.8

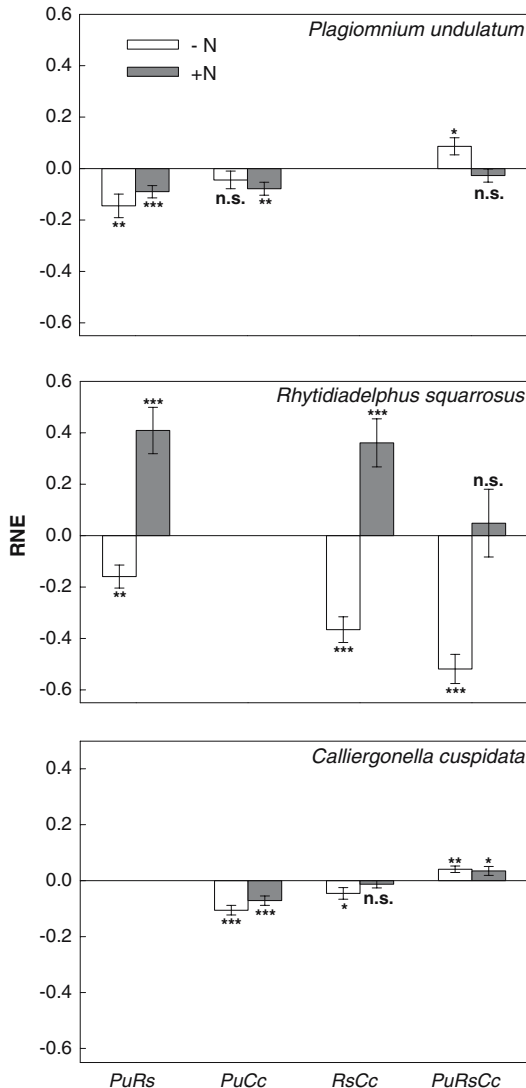


Fig. 2 Relative neighbour effect (RNE) of the three species on each other in two- and three-species mixtures. RNE values were calculated based on the species' relative growth rates. Positive values indicate facilitation, negative competition. Abbreviations refer to the initials of the species in the mixture. Error bars depict ± 1 SE

rather due to being able to maintain its growth rate of the unfertilised monocultures when facilitated by the presence of the other species. In fact, *R. squarrosus* grew less in all treatments compared to the unfertilised monoculture.

Competitive hierarchy

Figure 3 illustrates the strength and direction of species interactions in this experiment. For the unfertilised case, no clear competitive hierarchy emerged, due to the extremely similar performance of *C. cuspidata* and *P. undulatum*. *Calliergonella cuspidata* was superior to *R. squarrosus*, while the strength of competitive effects on each other was similar in the pair *P. undulatum* and *R. squarrosus*. All hierarchy was lost, however, in the fertilised case. This is due to the positive effect of both productive species on *R. squarrosus* and the small effect onto each other. The relationship of the three species cannot therefore be described as a simple linear hierarchy anymore.

Reciprocity of competition

Reciprocity means that the effect of species A on B should be positively correlated with the reciprocal of the effect of B on A. The correlation between the observed α_{ij} and $1/\alpha_{ji}$ in this study is negative, however (Fig. 4).

Transitivity and competition coefficients

The relative growth rates was used to calculate competition coefficients based on Lotka–Volterra-type competition. Under the assumption of perfect transitivity, the expected competition coefficient for a species mixture AB from the

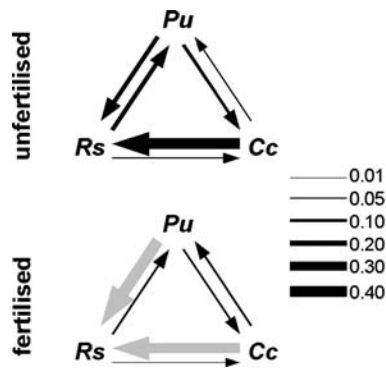


Fig. 3 Relative neighbour effects (RNE) between the three species under unfertilised and fertilised conditions. Line width indicates intensity of effect; grey bars indicate facilitation, black competition

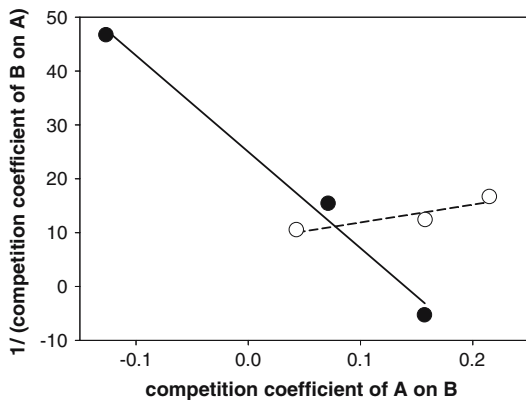


Fig. 4 Evaluation of reciprocity of competition effects. White dots and dashed line are from unfertilised treatments, black dots and solid line from fertilised. Under reciprocity one would expect a positive correlation. Here, $r = -0.77$

competition coefficients of the mixtures AC and CB can be calculated (see Freckleton and Watkinson 2001b and appendix). In this case, observed competition coefficients were *qualitatively* correct (in the sense that they indicated competition and facilitation correctly), but were *quantitatively* lower (Fig. 5). This difference was only significant in half of the cases, due to the high error attached to estimating competition coefficients under the transitivity assumption. The tentative conclusion is that this system does not show *quantitative* transitivity.

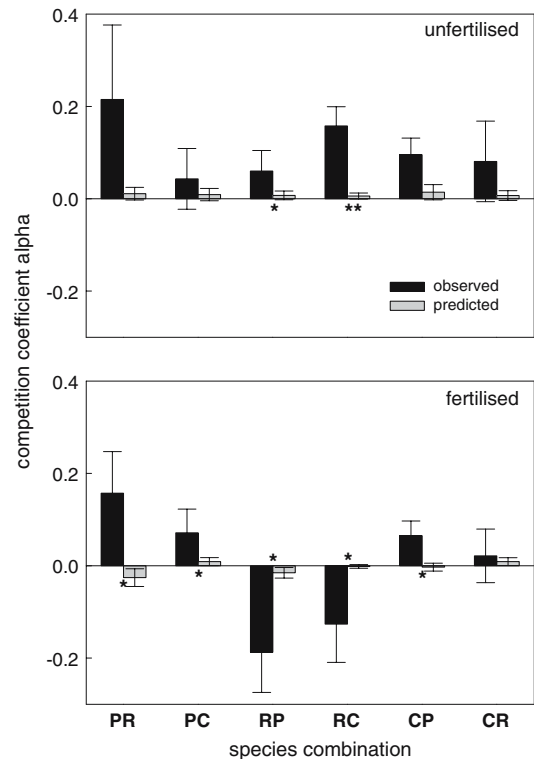


Fig. 5 Comparison of observed competition coefficients and those predicted assuming perfect transitivity. PR indicates the effect of species P on species R. Asterisks indicate significant differences at $P < 0.05$. Error bars depict ± 1 SE

Outcome of competition

In a community matrix-based analysis of competition outcome, all two-species mixtures were both stable and feasible (Table 2). The unfertilised three-species mixture is neither stable nor feasible (eigenvalues of the community matrix: $-0.019, -0.017, -0.001$; equilibrium biomass for *P. undulatum*, *R. squarrosus* and *C. cuspidata*, respectively: 2.12, 2.13, -0.04), but its fertilised counterpart again is both stable and feasible (eigenvalues: $-0.023 + 0.003i, -0.023 - 0.003i, -0.019$; equilibrium biomass: 3.21, 3.26, and 1.19).

Additivity of competitive effects

Predictions for the performance in the three-species mixtures based on Lotka–Volterra equations were qualitatively good (Fig. 6). In all cases

Table 2 Results of community matrix analysis for long-term coexistence

Species mixture (fertilisation)	Eigenvalues		Equilibrium biomass	
PR (0)	-0.019	-0.006	2.14	0.29
PC (0)	-0.019	-0.017	2.11	2.13
RC (0)	-0.019	-0.001	0.06	2.33
PR (1)	-0.019 + 0.003i	-0.019-0.003i	3.50	0.83
PC (1)	-0.022	-0.019	3.39	3.27
RC (1)	-0.022	-0.013	0.61	3.48

See Table 1 for species coding

observed RGR was higher than predicted (except *R. squarrosus* fertilised), indicating less competition than expected from Lotka–Volterra-type multi-species competition. Quantifying this difference using the non-additivity parameter of Dormann and Roxburgh (2005) yielded values between -0.11 and 0.47 (all significantly less than one), where a value of one would indicate a perfect match of predicted and observed values,

and values less than one indicate less-than-additive competitive effects.

Discussion

In line with other previous studies (reviewed e.g. by Goldberg et al. 1999) this study also shows that environmental perturbations can affect the competitive interrelations in a plant community. It shows that competitive interactions cannot necessarily be arranged in hierarchies, and consequences for coexistence after environmental perturbations may be difficult to predict. At present, however, too few experimental studies have been published that investigated the competition structure of plant communities to be able to generalise conclusions. The main aim of this study was to present a system and a methodology to address questions of competition in plant communities. Nonetheless, the different issues raised in the introduction with respect to the findings of these experiments are discussed here.

Hierarchy

Plagiomnium undulatum and *Calliergonella cuspidata* were virtually indistinguishable in their relative growth rate in mixture (Table 1). In direct competition *P. undulatum* exerts a slightly stronger effect on *C. cuspidata* than vice versa. However, *C. cuspidata*'s effect on *Rhytidiadelphus squarrosus* was more pronounced than *P. undulatum*'s (Fig. 3). *Plagiomnium undulatum*, on the other hand, was more reduced in performance by *R. squarrosus* than was *C. cuspidata*. Given the measurement errors attached to these calculations, the competitive hierarchy can be phrased as $Cc = Pu > Rs$.

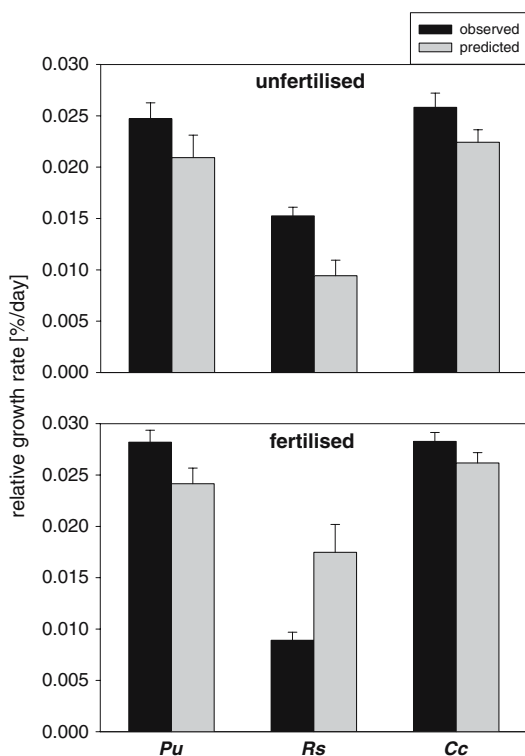


Fig. 6 Performance (relative growth rate) of the three moss species in three-species mixture, comparing the observed biomass (black) with that predicted from pairwise competition coefficients (grey). In no case is the difference significant. Note that error bars for the predictions are larger than for observed, due to error propagation involved in predicting mixture biomass

Under fertilisation, relative neighbour effects (RNE) were slightly reduced, but *R. squarrosus* now profited from the presence of its competitors (Fig. 2). The mechanism of this facilitation can be explained easily: *R. squarrosus* was physically shielded by both *C. cuspidata* and/or *P. undulatum* from the spray of nitrogen applications, which reduced its performance in directly exposed monocultures. Relative growth rates of *R. squarrosus* under competition plus fertilisation were lower than in the unfertilised monocultures (Table 1). This indicates that *C. cuspidata* and *P. undulatum* could not prevent all nitrogen from reaching *R. squarrosus* (leading to a growth reduction due to direct nitrogen damage) and/or that they did exert some competitive influence on *R. squarrosus*. The competitive effect of *R. squarrosus* on both other species was negligible (Fig. 3), and also *C. cuspidata* and *P. undulatum* barely impacted on each other. Hence, no competitive “hierarchy” exists for this situation.

As most concepts predict competition intensity to either increase (Grime 2001) or remain constant (Oksanen 1990; Tilman 1982) as productivity increases, the neutralisation of competition in the case of *R. squarrosus* is surprising. Callaway et al. (2002) report on shifts from competition to facilitation in alpine plant communities, i.e. positive neighbour effects in the face of physiological stress (see also Bertness and Hacker 1994; Hacker and Gaines 1997). In this study, this was the case for nitrogen-induced stress for *R. squarrosus*, illustrating that adaptations to a low-nitrogen environment make high nutrient loads a stress situation (Jones et al. 2002; Mitchell et al. 2004; Solga et al. 2005).

Reciprocity

The idea of reciprocity is based on resource competition (Tilman 1982): If a species A pre-empt resources from species B, B will grow less and in consequence affect the performance of A to a lesser extend. The stronger the pre-emption, the weaker B’s effect on A (this is also discussed under the keyword of asymmetric competition in the more recent literature, e.g. Bauer et al. 2004; Connolly et al. 1990; Rajaniemi 2003). In this study, the correlation between α_{ij} and $1/\alpha_{ji}$ is

negative (Fig. 4), lending no support to the idea of reciprocity. However, since I only compared three species pairs under two levels of fertilisation, the robustness of this correlation is extremely low. Moreover, the trend also changed between fertilisation treatments. The unfertilised pairs show no correlation, while in the fertilised case this is negative, resulting also in a net-negative trend across all data points. This pattern is clearly due to the facilitative effect of *P. undulatum* and *C. cuspidata* on *R. squarrosus*.

Transitivity

As can be expected from the lack of competitive “hierarchy”, interactions were not *quantitatively* transitive (sensu Freckleton and Watkinson 2001b). In most cases, however, competition coefficients indicate *qualitative* transitivity. The positive effects of *C. cuspidata* and *P. undulatum* on *R. squarrosus* under fertilisation make this particular community difficult to summarise. Possibly transitivity is a feature of competition-only communities. Competition is usually linked to biomass (Gaudet and Keddy 1988), while facilitation may have more to do with growth form (Brooker and Callaghan 1998). Hence, as experiments usually measure the net effect of plant–plant interactions, biomass-unrelated facilitative effects may unbalance transitivity. It becomes clear in any case that transitivity does not need to be a typical feature in moss communities.

Competition and community stability

The Lotka–Volterra approach to competition still forms the basis for most theoretical studies investigating community diversity and stability under environmental conditions or species compositions (for recent examples see Kokkoris et al. 1999, 2002; Lehman and Tilman 2000; Loreau 1998, 2004; Rozdilsky and Stone 2001; Wilson et al. 2003). In a recent study, for an artificial grassland system that one assumption of the Lotka–Volterra approach was showed, additivity of competitive effects, might not hold (Dormann and Roxburgh 2005). In the present study, growth rate predictions based on the LV model for three-

species mixture were relatively similar to those observed (Fig. 6). Nonetheless, fitting an additional parameter to quantify the mismatch showed that they were significantly deviating from the LV model. Real competition intensity was lower than expected. While for the grassland system of Dormann and Roxburgh (2005) spatial arrangement of plants may have caused some deviation, this is unlikely to be the case in the present study. In each tray, hundreds of moss fragments re-grew in well-mixed communities. This is one of the strong advantages of this system, since it allows a high number of individuals to be manipulated on a small spatial scale.

The observed competition coefficients indicate that all two-species mixtures allow for stable coexistence at equilibrium (Table 2). For the unfertilised three-species mixture, eigenvalue analysis of the community matrix indicates that coexistence of all three species is neither feasible (i.e. some species have sub-zero equilibrium biomass) nor stable (eigenvalues are not all negative). Fertilisation had a positive effect on community stability (now being both stable and feasible). This is a surprising finding, since fertilisation generally *decreases* species richness (Gough et al. 2000; Mittelbach et al. 2001; Waide et al. 1999). Probably this effect can be attributed to the switch in competitive to facilitative effects of *P. undulatum* and *C. cuspidata* onto *R. squarrosus*. Whether this system is ecologically fundamentally different from communities of vascular plants and closer related to the interactions nets of bryozoa, algae and ascidians (Buss 1986), whether the community matrix approach is unsuitable to predict system stability (Dormann and Roxburgh 2005), or whether the experiment simply did not run long enough to allow extrapolation remains an open question.

What are the mosses competing for?

Mosses take up most of their nutrients and water directly through their leaves, where they have very effective absorptive surfaces. Additionally, they can acquire nutrients from the soil. In this study, no attempt was made to distinguish the

source of nutrients for the different species. It seems plausible, however, to ascribe most nutrient uptake to the leaves, with only *P. undulatum* also extracting relevant amounts from the substrate. In contrast to the leafy *R. squarrosus* and *C. cuspidata*, *P. undulatum* supports a considerable biomass of rootlets and stems (“cauloid”) with high hydrological conductivity. Since bryophyte leaves (“phylloids”) serve the functions of assimilation, water and nutrient uptake, it is difficult to deduce what resources they are competing for. Their strong response to fertilisation indicates nutrient limitation. The etiolated appearance of phylloids on lower parts of the cauloid on the other hand suggests light limitation, and hence also light seems to be a likely limiting factor. Van der Hoeven et al. (1998) report a high sensitivity of *R. squarrosus* for low levels of irradiance, which also hints at light competition. In either case, competition would be for space in the top level of the canopy.

The response of *Rhytidiadelphus squarrosus*

To someone familiar with *R. squarrosus* the strongly negative response of this species to nitrogen fertilisation may be surprising. *Rhytidiadelphus squarrosus* is a notorious species of lawns across temperate Europe and rather resilient to gardener’s removal efforts. Since private lawns are usually fertilised the response of *R. squarrosus* in this study seems not to be in line with its growth performance in gardens. However, after fertilisation *R. squarrosus* also briefly disappears in garden lawns, but re-colonises quickly. The other explanation is that *R. squarrosus* responded badly to the fragmentation process during preparation of stock solutions. Although it was the first of the three species to re-grow (after about 1 week), it did so only very slowly.

This should not invalidate any of the results in this study. A naturally slow-growing species may have yielded the same behaviour and the significant responses to competition and fertilisation indicate that *R. squarrosus* was sensitive to its environment.

Conclusion

This study showed that moss communities are a suitable system to address questions of community composition, competition effects and theoretical models for species coexistence. The lack of several features of higher plant communities, such as transitivity, competitive hierarchies or reciprocity, casts doubts on the general validity of such community traits. Clearly more studies on multi-species competition are required to address this issue. The study also shows that detailed experimental investigations may reveal different patterns than observational studies or long-term field experiments, hence calling for a closer integration of theory, lab and field experiments when attempting to unravel the implications of competitive and facilitative interactions for community composition.

Acknowledgements I thank Nikolai Köbernic for his help in running and harvesting the experiment, Martin Freiberg, Matthias Schwieger and the staff of the Botanical Garden Leipzig for help with experimental setup, Carsten Vogt for logistic support and Christian Rixen for sharing his experience in moss blending. Comments by Justin Calabrese, Christian Rixen and two anonymous referees considerably improved a previous version of this manuscript.

Appendix

Deriving the equilibrium solution for Lotka–Volterra-type competition between two species

Starting with a two species LV-model of species A and B, with growth rate r , carrying capacity K , competition coefficient α and performance measure w (e.g. biomass, RGR or alike):

$$dw_{AB}/dt = r_A w_{AB}/K_A (K_A - w_{AB} - \alpha_{AB} w_{BA})$$

$$dw_{BA}/dt = r_B w_{BA}/K_B (K_B - w_{BA} - \alpha_{BA} w_{AB}).$$

At equilibrium $dw/dt = 0$. As r , w and $K > 0$, it follows that

$$(K_A - w_{AB} - \alpha_{AB} w_{BA}) = 0 \quad \text{and}$$

$$(K_B - w_{BA} - \alpha_{BA} w_{AB}) = 0,$$

hence $\alpha_{AB} = (K_A - w_{AB})/w_{BA}$ and $\alpha_{BA} = (K_B - w_{BA})/w_{AB}$

Relating α_{ij} from the Lotka–Volterra equation to ε_{ij} from Freckleton and Watkinson (2001b)

Freckleton and Watkinson (2001b) start with the hyperbolic growth model, which is based on the number of individuals as performance measure. It cannot be directly applied to biomass, as it assumes a trade-off between individual biomass and density. In this study I have no information about the number of individuals in the trays and hence again use the Lotka–Volterra formulation:

$$dw_{AB}/dt = r_A w_{AB}/K_A (K_A - w_{AB} - \alpha_{AB} w_{BA}).$$

However, now I introduce α_{ii} to indicate intraspecific competition:

$$dw_{AB}/dt = r_A w_{AB}/K_A (K_A - \alpha_{AA} w_{AB} - \alpha_{AB} w_{BA}).$$

In analogy to Freckleton and Watkinson (2001b), I transform:

$$dw_{AB}/dt = r_A w_{AB}/K_A (K_A - \alpha_{AA} (w_{AB} - \alpha_{AB}/\alpha_{AA} w_{BA}))$$

The equivalence coefficient ε_{ij} is now defined as the ratio of α_{ij} and α_{ii} . Since I have no information on the strength of intraspecific competition, I set $\alpha_{ii} = 1$ and hence $\varepsilon_{ij} = \alpha_{ij}$. Both in the analysis of Freckleton and Watkinson (2001b) and in this study, ε_{AB} represents the competitive effect of species B on species A in equivalents of A. If, for example, adding 1 g of species A would lead to a reduction in final biomass of A by 0.5 g, while adding 1 g of species B would lead to a 2 g reduction, $\varepsilon_{AB} = 4$, as 1 g of B has the same effect as 4 g of A.

For perfect transitivity of a competitive hierarchy, Freckleton and Watkinson (2001b) show

that $\varepsilon_{ik} = \varepsilon_{ij} \cdot \varepsilon_{jk}$. In this study, I use competitive coefficients α_{ij} instead.

Estimating competition coefficients under the assumption of perfect transitivity

The competition coefficient α_{AB} is defined as $\alpha_{AB} = (K_A - w_{AB})/w_{BA}$ (see above).

In analogy: $\alpha_{BC} = (K_B - w_{BC})/w_{CB}$.

Perfect transitivity assumes that $\alpha_{AC} = \alpha_{AB} \cdot \alpha_{BC}$, hence:

$$\alpha_{AC} = (K_A - w_{AB})/w_{BA} (K_B - w_{BC})/w_{CB}.$$

When calculating the estimated α_{AC} along this formula, errors in all six variables propagate into the estimate of α_{AC} . There are $5^6 = 15625$ possible combinations of values from this study (5 replicates for the 6 variables). I used the mean and standard error (standard deviation divided by the square root of 5) of these 5^6 values in Fig. 4.

In contrast, the observed α_{AC} depends only on three variables (K_A , w_{AC} and w_{CA}) and can be determined with greater accuracy ($5^3 = 125$ values).

References

- Aarssen LW (1988) 'Pecking order' of four plant species from pastures of different ages. *Oikos* 51:3–12
- Archibold OW (1994) *Ecology of world vegetation*. Chapman & Hall, London
- Bauer S, Wyszomirski T, Berger U, Hildenbrandt H, Grimm V (2004) Asymmetric competition as a natural outcome of neighbour interactions among plants: results from the field-of-neighbourhood modelling approach. *Plant Ecol* 170:135–145
- Bertness MD, Hacker SD (1994) Physical stress and positive associations among marsh plants. *Am Natural* 144:363–372
- Brooker RW, Callaghan TV (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81:196–207
- Buss LW (1986) Competition and community organization on hard surfaces in the sea. In: Diamond JM, Case TJ (eds) *Community ecology*. Harper & Row, New York, pp 517–536
- Callaway RM, Brooker RW, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET, Armas C, Kikodze D, Cook BJ (2002) Positive interactions among alpine plants increase with stress. *Nature* 417:844–848
- Case TJ (2000) *An illustrated guide to theoretical ecology*. Oxford University Press, Oxford
- Case TJ, Bender EA (1981) Testing for higher-order interactions. *Am Natural* 118:920–929
- Connolly J, Wayne P, Bazzaz FA (2001) Interspecific competition in plants: how well do current methods answer fundamental questions? *Am Natural* 157:107–112
- Connolly J, Wayne P, Murray R (1990) Asymmetric competition between plant species. *Oecologia* 108:311–320
- Diamond JM (1986) Overview: Laboratory experiments, field experiments, and natural experiments. In: Diamond JM, Case TJ (eds) *Community ecology*. Harper & Row, New York, pp 3–22
- Dierßen K (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. J. Cramer, Berlin
- Dormann CF, Roxburgh SH (2005) Experimental evidence rejects classical modelling approach to coexistence in plant communities. *Proc R Soc London Ser B* 272:1279–1285
- Fowler N (1981) Competition and coexistence in a North Carolina grassland. II. The effect of the experimental removal of species. *J Ecol* 69:843–854
- Frahm J-P, Frey W (1992) *Moosflora*, 3rd edn. Ulmer, Stuttgart
- Frean M, Abraham ER (2001) Rock-scissors-paper and the survival of the weakest. *Proc R Soc London Ser B* 268:1323–1327
- Freckleton RP, Watkinson AR (2000) Designs for greenhouse studies of interactions between plants: an analytical perspective. *J Ecol* 88:386–391
- Freckleton RP, Watkinson AR (2001a) Nonmanipulative determination of plant community dynamics. *Trends Ecol Evol* 16:301–307
- Freckleton RP, Watkinson AR (2001b) Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. *Ecol Lett* 4:348–357
- Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature* 334:242–243
- Gibson DJ, Connolly J, Hartnett DC, Weidenhamer JD (1999) Designs for greenhouse studies of interactions between species. *J Ecol* 87:1–16
- Gleason HA (1926) The individualistic concept of plant association. *Bull Torrey Bot Club* 53:7–26
- Goldberg DE (1994) Influence of competition at the community level: an experimental version of the null models approach. *Ecology* 75:1503–1506
- Goldberg DE, Landa K (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *J Ecol* 79:1013–1030
- Goldberg DE, Rajaniemi T, Gurevitch J, Stewart-Oaten A (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118–1131
- Goldberg DE, Turkington R, Olsvig Whittaker L (1995) Quantifying the community-level consequences of competition. *Folia Geobot Phytotaxon* 30:231–242

- Gotelli N (1995) A primer of ecology. Sinauer Associates, Sunderland, Massachusetts
- Gough L, Osenberg CW, Gross KL, Collins SL (2000) Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos* 89:428–439
- Grace JB (1995) On the measurement of plant competition intensity. *Ecology* 76:305–308
- Grime JP (2001) Plant strategies and vegetation processes, 2nd edn. John Wiley, Chichester
- Hacker SD, Gaines SD (1997) Some implications of direct positive interactions for community species diversity. *Ecology* 78:1990–2003
- Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn JA, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras A-SD, Spehn EM, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286:1123–1127
- Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton Univ. Press, Princeton
- Hutchings MH (1997) The structure of plant populations. In: Crawley MJ (ed) *Plant ecology*, 2nd edn. Blackwell, Oxford, pp 325–358
- Istock CA (1977) Logistic interaction of natural populations of two species of waterboatmen. *Am Natural* 111:279–287
- Jones MLM, Oxley ERB, Ashenden TW (2002) The influence of nitrogen deposition, competition and desiccation on growth and regeneration of *Racomitrium lanuginosum* (Hedw.) Brid. *Environ Pollut* 120:371–378
- Keddy PA (1989) *Competition*. Chapman & Hall, London
- Keddy PA, Shipley B (1989) Competitive hierarchies in herbaceous plant communities. *Oikos* 54:234–241
- Kokkoris GD, Jansen VAA, Loreau M, Troumbis AY (2002) Variability in interaction strength and implications for biodiversity. *J Anim Ecol* 71:362–371
- Kokkoris GD, Troumbis AY, Lawton JH (1999) Patterns of species interaction strength in assembled theoretical competition communities. *Ecol Lett* 2:70–74
- Kooijman AM, Bakker C (1995) Species replacement in the bryophyte layer in mires—the role of water type, nutrient supply and interspecific interactions. *J Ecol* 83:1–8
- Lehman CL, Tilman D (2000) Biodiversity, stability, and productivity in competitive communities. *Am Natural* 156:534–552
- Levins R (1968) *Evolution in changing environments*. Princeton University Press, Princeton
- Loreau M (1998) Ecosystem development explained by competition within and between material cycles. *Proc R Soc London Ser B* 265:33–38
- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611
- Markham JH, Chanway CP (1996) Measuring plant neighbour effects. *Funct Ecol* 10:548–549
- McAlister S (1995) Species interactions and substrate-specificity among log-inhabiting bryophyte species. *Ecology* 76:2184–2195
- Mitchell RJ, Sutton MA, Truscott A-M, Leith ID, Cape JN, Pitcairn CER, Van Dijk N (2004) Growth and tissue nitrogen of epiphytic Atlantic bryophytes: effects of increased and decreased atmospheric N deposition. *Funct Ecol* 18:322–329
- Mittelbach G, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dobson SI, Gough L (2001) What is the observed relationship between species richness and productivity? *Ecology* 82:2381–2396
- Mulder CPH, Uliassi DD, Doak DF (2001) Physical stress and diversity–productivity relationships: the role of positive interactions. *Proc Natl Acad Sci USA* 98:6704–6708
- Mulligan RC, Gignac LD (2002) Bryophyte community structure in a boreal poor fen II: interspecific competition among five mosses. *Can J Bot-Revue Canadienne De Botanique* 80:330–339
- Oksanen L (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace JB, Tilman D (eds) *Perspectives in plant competition*. Academic Press, London, pp 445–474
- R Development Core Team (2004) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>
- Rajaniemi TK (2003) Explaining productivity–diversity relationships in plants. *Oikos* 101:449–457
- Rees M, Condit R, Crawley MJ, Pacala S, Tilman D (2001) Long-term studies of vegetation dynamics. *Science* 293:650–655
- Rees M, Grubb PJ, Kelly D (1996) Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *Am Natural* 147:1–32
- Richardson DHS (1981) *The biology of mosses*. Blackwell, Oxford
- Rixen C, Mulder CPH (2005) Improved water retention links high species richness with increased productivity in arctic tundra moss communities. *Oecologia* 146:287–299
- Roscher C, Schumacher J, Baade J, Wilcke W, Gleixner G, Weisser WW, Schmid B, Schulze ED (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic Appl Ecol* 5:107–121
- Roxburgh SH, Wilson JB (2000) Stability and coexistence in a lawn community: mathematical prediction of stability using a community matrix with parameters derived from competition experiments. *Oikos* 88:395–408
- Rozdilsky ID, Stone L (2001) Complexity can enhance stability in competitive systems. *Ecol Lett* 4:397–400
- Shipley B (1993) A null model for competitive hierarchies in competition matrices. *Ecology* 74:1693–1699
- Solga A, Burkhardt J, Zechmeister HG, Frahm JP (2005) Nitrogen content, N-15 natural abundance and

- biomass of two pleurocarpous mosses *Pleurozium schreberi* (Brid.) Mitt. and *Scleropodium purum* (Hedw.) Limpr. in relation to atmospheric nitrogen deposition. *Environ Pollut* 134:465–473
- Steel JB, Wilson JB, Anderson BJ, Lodge RHE, Tangney RS (2004) Are bryophyte communities different from higher-plant communities? Abundance relations. *Oikos* 104:479–486
- Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ
- Tilman D, Wedin D (1991) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72:685–700
- Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718–720
- Tirado R, Pugnaire FI (2005) Community structure and positive interactions in constraining environments. *Oikos* 111:437–444
- van der Hoeven EC, Korporaal M, Van Gestel E (1998) Effects of simulated shade on growth, morphology and competitive interactions in two pleurocarpous mosses. *J Bryol* 20:301–310
- Waide RB, Willig MR, Steiner CF, Mittelbach G, Gough L, Dodson SI, Juday GP, Parmenter R (1999) The relationship between productivity and species richness. *Annu Rev Ecol Syst* 30:257–300
- Wedin DA, Tilman D (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecol Monogr* 63:199–229
- Weigelt A, Jolliffe P (2003) Indices of competition. *J Ecol* 91:707–720
- Wilson JB, Roxburgh SH (1992) Application of community matrix theory to plant competition. *Oikos* 65:343–348
- Wilson JB, Steel JB, Newman JE, Tangney RS (1995) Are bryophyte communities different? *J Bryol* 18:689–705
- Wilson WG, Lundberg P, Vázquez DP, Shurin JB, Smith MD, Langford W, Gross KL, Mittelbach GG (2003) Biodiversity and species interactions: extending Lotka–Volterra community theory. *Ecol Lett* 6:944–952
- Wootton JT (1994a) The nature and consequences of indirect effects in ecological communities. *Annu Rev Ecol Syst* 25:443–466
- Wootton JT (1994b) Putting the pieces together—testing the independence of interactions among organisms. *Ecology* 75:1544–1551
- Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. *J Biol, Osaka City Univ* 14:107–129
- Zamfir M, Goldberg DE (2000) The effect of initial density on interactions between bryophytes at individual and community levels. *J Ecol* 88:243–255