

On community matrix theory in experimental plant ecology

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In multi-species communities the stability of a system is difficult to assess from field observations. This is the case for example for competitive interactions in plant communities. If a mathematical model can be formulated that underlies the processes in the community, a community matrix can be constructed whose elements represent the effects of each species onto every other (and itself) at equilibrium. The most common competition model is the Lotka–Volterra equation set. It contains interspecific competition coefficients to represent the interactions between species. In plant community ecology several attempts have been made to quantify competitive interactions and to assemble a community matrix, so far with limited success. In this paper we discuss a method to use pairwise interaction coefficients from experimental plant communities to analyse feasibility and stability of multi-species sets. The approach is contrasted with that of Wilson and Roxburgh (1992) and is illustrated using data from Roxburgh and Wilson (2000a). Results from Wilson and from this study differ (some times substantially), with our approach being more pessimistic about stability and coexistence in plant communities.

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Community matrix theory (CMT) uses the analytical description of species interactions to investigate the stability of the system (Levins 1968, May 1973). These interactions may be across trophic levels (i.e. predation, parasitism, pollination) or within trophic levels (competition, facilitation). CMT offers a methodology to analyse the complex interaction of an entire set of species. Despite its straightforward mathematics and its wide utilisation in theoretical ecology, CMT has received very little attention by field ecologists (for one of the few examples see Schmitz 1997).

In 1992, Wilson and Roxburgh advocated the idea of using community matrix theory to assess stability of plant communities (i.e. coexistence probability). As Wilson and Roxburgh (WR hereafter) correctly pointed out, it has been ‘very rarely [...] possible to test the commu-

nity matrix approach on real organisms’ (p. 344), because the experimental data required for this approach have not been available. One such test has been performed by the same authors (Roxburgh and Wilson 2000b). None of the plant communities analysed by WR was stable according to community matrix methodology. This, in part, is due to problems of the WR-approach to assess the stability and feasibility of a community matrix. In this paper, we want to address some of these problems and assess the consequences for stability analysis in plant communities.

This paper falls into three sections: in the following paragraphs we first briefly explain ‘community matrix theory’ as far as it is relevant to stability of plant communities. Next, we will address some problems of the analysis suggested by Roxburgh and Wilson (2000a, 2000b) and present an alternative directly based on a theoretical model

of plant interactions, illustrating the approach with experimental data. Finally, we will briefly review community matrix studies in plant ecology.

Community matrix theory and the stability of communities

There are several introductions to CMT (Pimm 1982, Case 2000), and here we only describe those elements needed to understand how to apply CMT to experimental plant ecology.

The main idea is that a stable community with n members will return to equilibrium after minor disturbances (i.e. resilience or steady-state equilibrium; this definition of stability is different from stability in the sense of resistance, e.g. to invaders). Increasing (or decreasing) the abundance of a member of that community, w_i , will affect the other member according to the interaction strength between them. This interaction strength is quantified in the 'community matrix' S , an $n \times n$ matrix, with elements called s_{ij} . Imagine a community following competitive Lotka–Volterra dynamics:

$$dw_i/dt = (r_i/K_i) w_i (K_i - w_i - \sum \alpha_{ij} w_j) \quad (1)$$

It can be shown (Case 2000) that in this situation the elements for the community matrix are $s_{ii} = -(r_i/K_i)N_i^*$ and $s_{ij} = -(r_i/K_i)N_j^*\alpha_{ij}$, where N_i^* is the equilibrium density of species N_i , K_i the carrying capacity and r_i the growth rate. The community is stable, if the real parts of all eigenvalues of the community matrix S are negative, which can be interpreted as the existence of coexistence equilibrium. However, that the real part of the leading eigenvector is negative is no guarantee that this equilibrium is feasible, i.e. that all species have positive biomass under equilibrium conditions.

The vector of equilibrium densities N^* is calculated according to $N^* = K \alpha^{-1}$ (Case 2000), using the inverse of the competition matrix, α^{-1} and the vector of carrying capacities. $\alpha = (\alpha_{ij})$, $i, j = 1, \dots, N$, contains all pairwise interaction coefficients, with the diagonal elements denoting the intraspecific competition coefficients equal unity. Traditionally, interaction coefficients α are referred to as competition coefficient because a competitive relationship was assumed. We shall relax this assumption later on to negative interaction coefficients, i.e. facilitation between species. For simplicity, we refer to interaction experiments as competition experiments, as most of the rest of the experimental plant ecology literature, although some interactions may indeed be facilitative (and models would then become co-opetition models: López-Gómez and Molina-Meyer 2007). The main point is that information on r_i , K_i and α_{ij} are available from pairwise competition experiments: K_i is the maximum biomass of species i in monoculture, and the elements of α , α_{ij} , can be calculated on the

basis of the Lotka–Volterra equation system as detailed below. If all elements of N^* are greater than 0, i.e. all species have positive equilibrium biomass, then the equilibrium is biologically feasible.

Problems with the application of CMT to experimental competition data, with special respect to plant communities

The most fundamental problem is the specification of the interaction equations. It has to be stressed that although Lotka–Volterra-models are the most commonly used descriptions of species interactions in the context of CMT, the approach is not restricted to them. Most ordinary differential or difference equation systems can form the basis for the community matrix elements. In fact, it is most likely that Lotka–Volterra will not be a good description of plant competition (Dormann and Roxburgh 2005), and that different representations of plant competition have to be used (Firbank and Watkinson 1985, Damgaard 1998).

In this section we want to first focus on conceptual rather than practical difficulties (such as experimental design, random selection of species, replication, etc). In a second step we will then turn to practical issues and present an example.

The data needed to calculate the elements of a community matrix comprise at least maximum biomass for all species grown in monoculture, growth rates in monocultures and competition coefficients among all species pairs.

How to 'measure' competition coefficients?

WR argue that as only a single, final harvest took place in the experiments they use for illustration we cannot calculate growth rates for the species, which is needed for stability analysis. Thus, they conclude, the CMT-approach must be modified. This issue raises two points: 1) how can we measure competition coefficients? and on a more technical note, 2) because we cannot calculate growth rates based on only initial and final harvest data, how can we deal with this issue? Let us look at the first question first; the second question is addressed in the next section.

Imagine an experiment designed to generate data for the competition (and community) matrix, say for a small grassland community, where few species represent 95% of total aboveground biomass. Some two-species combinations will be of a rather tall, clonal and dominant species and some relatively small, non-clonal and subdominant species. When grown in a pot in a greenhouse together, it is only a question of time until the taller will eventually displace the smaller one. Now the obvious question arises: when does one best measure competition intensity? If measurements are taken, say, within the first six months, interference may be limited. Waiting for an entire

year or two will show the final outcome already, with no sub-dominant species surviving. Hence, no biomass measurements for the sub-dominant species can be taken to calculate competition coefficients.

This thought experiment identifies the problem related to the density-dependency of the competition coefficient. If an equilibrium for the entire community exists, it would probably be best to have a biomass ratio between the two species similar to that at equilibrium. Usually there is a real community we want to approximate with our matrix approach. If so, we can try to establish biomass ratios in pots similar to those observed in our community. However, at equilibrium another five species are interfering simultaneously, and the effectively interacting biomasses for our two species may be rather different from what we may observe in the field.

There is no optimum solution to this problem. Usually biomass measurements are taken after one season (6–8 months), one or two years. Species will by then be tall enough to compete with each other, while at the same time the dominant hasn't yet driven the sub-dominant to extinction. There are no data available in the literature of how competition coefficients change over time during plant establishment.

How to analyse competition and community matrices for stability?

Calculating competition coefficients

Competition coefficients transform the effect per unit biomass of the competitor into effect per biomass equivalent of the target species. If, for example, species B suppresses the growth of A by 1 g for each gram of B, while A suppresses its own growth by only 0.5 g per gram of A, then the competition coefficient $\alpha_{AB} = 2$. B is (on a per gram basis) competing twice as strongly with A than A with itself. It follows that α_{AB} is calculated as the reduction in biomass of A in mixture with B relative to monocultures of A, divided by the biomass of B: $\alpha_{AB} = (K_A - w_A)/w_B$. This formula can be derived from the Lotka–Volterra equations for competition between two species (Istock 1977). Starting with equation (1), at equilibrium we obtain (for species A) $(K_A - w_A - \alpha_{AB} w_B) = 0$ (as r_A, w_A are positive) and hence $\alpha_{AB} = (K_A - w_A)/w_B$.

These data should be available from every competition experiment with monocultures and two-species mixtures. As discussed above the values for w_A and w_B will depend on when during the experiment the biomass measurements were taken.

Constructing the community matrix

As noted above, the community matrix can be constructed from the competition matrix and the growth rate/carrying capacity-vector. However, we cannot calculate r by fitting a logistic growth function, as the function has three pa-

rameters, but we only have two points: the problem is that biomass was often measured only at the end of the experiment and it is unknown when biomass values reached that final value. For some species, growth may be extremely fast during the first few weeks, thus levelling off at equilibrium already long before the end of the experiment. Fitting a logistic growth curve to the final biomass at the time of harvest will severely over- or underestimate real growth rates. For many species, growth rates have been measured and published (Grime et al. 1988), but mostly under different growing conditions. Deriving a good estimate for r seems to be a core problem in the construction of the community matrix (Roxburgh 1994).

Effect of growth rate on the eigenvalues of the community matrix

Can we get around this problem by ignoring it? If we discard r from the entry s_{ij} in the community matrix (i.e. set $r = 1$), will the eigenvalues change their sign? To address this question we randomly assembled community matrices for seven competing species, with and without factoring in a value for r , and compared their eigenvalues. 31% (± 3.9 SD) of all stable matrices with r set to 1 became unstable when a realistic value for r was chosen. These results were independent on the sign-structure of the competition matrix, i.e. higher percentages of negative competition coefficients (i.e. facilitative interactions) had the same percentage of sign changes.

The take-home-message from this simulation exercise is that to evaluate stability and feasibility, however, we do need the complete community. The values for α and K are critical but should also be available from experiments; N^* can be computed from the competition matrix and the carrying capacity vector. However, r has a major impact on the signs of the eigenvalues.

We can take this evaluation a step further and 'split' the community matrix entries into the competition matrix containing only the α_{ij} and another matrix containing the rest ($-r_i N_i / K_i$). We ran a simulation comparing the signs of the leading eigenvalues for the competition matrix alone with that of the complete community matrix. The results indicate that the competition matrix alone leads to correct prediction of stability of the community matrix in only 41% of the cases. In 59% (± 3.8 SD) of the cases did the competition matrix give the wrong indication of stability of the community matrix. This result was again insensitive to the percentage of facilitative interactions. This means stability evaluation can not proceed on the competition matrix alone.

Community size and uncertainties associated with measurements of growth rate, competition coefficients and carrying capacities will affect eigenvalues of the community matrix. Even small changes in community matrix entries can modify its eigenvalues, and this effect scales as a power function with community size (Ciarlet 1985). Already with seven species is the imprecision of experimen-

tal results enough to yield stable and unstable matrices (Roxburgh and Wilson 2000b).

WR suggested a different way to derive the values for the community matrix. They used relative yield per plant (RYP), i.e. the biomass ratio of the target species i in competition with species j and in monoculture: $RYP_{ij} = w_{ij}/w_i$. These values are 1 for no competitive effect of j on i , and less than 1 for competitive effects. In the community matrix, WR argue, lack of competition is represented by a value of 0, and negative values indicate competition. Thus they suggest a \log_2 -transformation to achieve this effect. In consequence, the entries in their community matrix are: $s_{ij} = \log_2 RYP_{ij} = \log_2 (w_{ij}/w_i)$. Their analysis then proceeds with the calculation of the eigenvalues of the community matrix, but does not allow for an assessment of the feasibility of the equilibrium, i.e. no equilibrium biomass for the species can be calculated.

There are two points of criticism: firstly, the non-linear transformation of RYP-values has no theoretical basis and is thus not guaranteed to produce values qualitatively similar to the 'real' community matrix entries. Moreover, there is no obvious reason to use RYP, rather than biomass differences between mixture and monoculture. Figure 1 shows that for the data presented in the example below there is no reasonable relation between the Lotka–Volterra-based community matrix entries and WR's entries. (We present real data rather than simulations here, as communities show several features likely to influence the comparison, such as transitivity and asymmetry of competition.) We would therefore be very sceptical about using the proposed shortcut. Secondly, if we cannot assess the feasibility of equilibrium, only little is gained from knowing if it would be stable (Table 3).

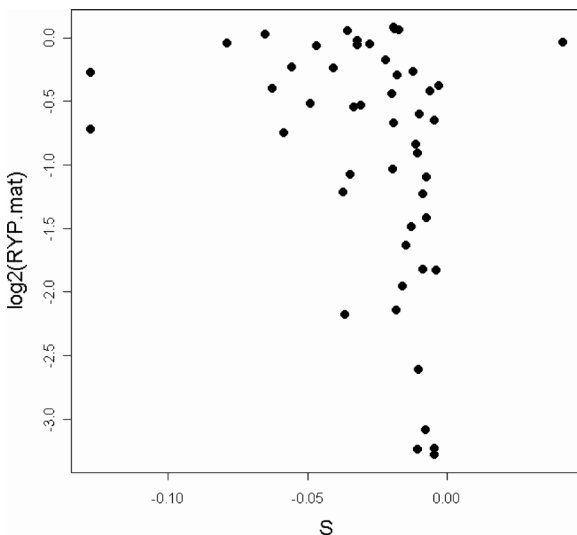


Fig. 1. A comparison of community matrix (S) entries with those of the RYP-matrix. The values are only weakly but negatively correlated (Pearson's $r = -0.304$, $p < 0.05$; Spearman's rank $r = -0.422$, $p < 0.01$).

In summary: to calculate feasibility and stability of competitive plant communities we can do without exact values for growth rates only for small communities (i.e. less than four to five species). Even in these species-poor situations we can not simplify the approach to determining the stability of the community by assessing the stability of the competition matrix alone.

An example

The following example is based on data published in Roxburgh and Wilson (2000a) and Roxburgh (1994). They grew seven species in pots, both in monocultures and in all pairwise combinations (three seedlings of each species per pot; additive design). Each treatment was replicated 10 times. After one year they harvested aboveground biomass. All calculations in the following paragraphs are based on these measurements and were performed using the software package R (function names given in parentheses, R Development Core Team 2008).

The values for carrying capacity of species i are simply the biomass (in g) of i in monoculture at the final harvest (for the species *Agrostis capillaris*, *Festuca rubra*, *Hydrocotyle heteromeria*, *Holcus lanatus*, *Prunella vulgaris*, *Ranunculus repens*, *Trifolium repens*): $K = (20.4, 10.5, 6.0, 20.5, 12.8, 10.0, 21.3)$.

Roxburgh and Wilson (2000b) could show that this biomass is indeed indistinguishable from the final yield of monocultures with double initial density and from monocultures grown for two years, thus that the 'law of constant final yield' holds independent of initial conditions, and that the experiment ran long enough to yield this level of biomass.

Competition coefficients α_{AB} can best be derived by fitting the non-linear function $w_A = K_A' - \alpha_{AB} w_B$, using the values of all replicates (nls; K_A' is the mean of carrying capacities). This fitting assumes normally distributed errors, which was the case for all models of this dataset. The calculated values are presented in Table 1 as the competition matrix. Note that by definition $\alpha_{ii} = 1$ (i.e. w_A in formula (1) and (2) has no coefficient). The diagonal entries accordingly have no error attached to them. Alternatively you can calculate α_{AB} using only the means for K_A , w_A and w_B in the last formula.

As explained above, we need to calculate growth rates to investigate stability and feasibility of the community. The following two paragraphs shall illustrate how to do it, and also explain the method used to compare the WR analysis with the method presented in this paper.

To calculate growth rates of the seven species from the data in this experiment two assumptions have to be made: 1) final yield was reached, and 2) final yield was reached exactly at the time of final harvest. Especially the second assumption is likely to be violated. For some species final biomass will be reached somewhat earlier or later than the time of harvest. Calculating growth rates under the assumption that plants reached final yield four weeks earlier

than the harvest did not greatly affect growth rates, however (Roxburgh 1994).

Growth rates can be calculated fitting a logistic growth-curve through the initial and final biomass data. This can be achieved by dynamically optimising the value for r in the differential equation: $dw_A/dt = r/K(K - w_A)$. In this example step-size for the differential equation evaluation function (lsoda) was set to one week (i.e. 52 time steps). An optimisation procedure (optim) can be used to minimise the difference between observed and fitted values (using initial biomass as $w_A(0)$ and final biomass as $w_A(52)$). This yields the growth rate of species A in monoculture. The values for r are: Ac: 0.367, Fr: 0.359, Hh: 0.382, Hl: 0.367, Pv: 0.355, Rr: 0.321, Tr: 0.351.

We can now calculate the vector of equilibrium biomass N^* of the seven species:

$$N^* = K \alpha^{-1} = \begin{pmatrix} 20.4 \\ 10.5 \\ 6.0 \\ 20.5 \\ 12.8 \\ 10.0 \\ 21.3 \end{pmatrix} * \begin{pmatrix} 3.77 & & & & & & \\ & \ddots & & & & & \\ & & \ddots & & & & \\ & & & \ddots & & & \\ & & & & \ddots & & \\ & & & & & \ddots & \\ & & & & & & 2.63 \end{pmatrix} = \begin{pmatrix} -3.95 \\ 13.23 \\ 1.44 \\ 39.87 \\ -40.93 \\ 1.41 \\ 27.56 \end{pmatrix}$$

We see that species 1 and 5 have negative biomass values. This indicates that the equilibrium is biologically infeasible. There is hence no point in analysing the stability of this equilibrium point. Instead, we now would do the same for all six-species mixtures and so forth until we know which species combinations have a feasible equilibrium. For those we then continue with the local stability analysis (Table 2, 3).

Here, we perform a stability analysis for the complete seven-species set for illustrational purposes only. This requires the calculation of the eigenvalues of the competition matrix (eigen). We yield (in decreasing absolute length of the eigenvalue): 6.048, 0.838, 0.432, -0.245 , 0.082, $0.001+0.06i$, $0.001-0.06i$ ($i = \sqrt{-1}$; representing the imaginary part of the eigenvalue). As some real parts of the eigenvalues are negative, but stability requires all of them to be negative, the seven-species mixture is instable at equilibrium

(which, in addition, was infeasible). The analysis of all subsets of this dataset is presented in the next section.

A re-evaluation of available competition data

There are only few data sets published that allow a feasibility and stability analysis. Wilson and Roxburgh (1992) present an analysis of a study by Aarssen (1988) and of Johannsson and Keddy (1991), of which the latter is unsuitable for the method proposed here, as only data on relative yield per plant are presented. Another data set is available from Roxburgh and Wilson (2000a), which is with seven species also the most species-rich community investigated to date. In neither of the two data sets is any interaction coefficient negative (Table 1). Dormann (2007) reports both stability and feasibility explicitly, so his results will only be re-iterated here.

What these data suggest is that stable coexistence at equilibrium of more than three species should not be expected in competitive communities with moderate to high competition coefficients, if Lotka–Volterra dynamics underly plant population dynamics (Kokkoris et al. 1999, 2002). Taking into account that data sets are from communities that show coexistence at even higher species richness since decades (albeit with slight changes in the case of Aarssen's pastures), we can deduce that the forces counteracting competition, and thereby allowing coexistence, must be relatively strong. A plethora of coexistence mechanisms in the face of competition have been suggested (most noteworthy spatial heterogeneity of resources and thus competition intensity; reduction in competition intensity by herbivores or pathogens; competition/colonisation tradeoff; periodic or stochastic disturbances; and environmental stress). Most of them cannot readily be included into community matrix analysis, due to the spatial or temporal representation of structuring forces.

Comparing feasibility and stability limitations to coexistence

Table 3 shows for the Aarssen (1988) data that feasibility more often is the 'killing criterion' for coexistence than

Table 1. Competition coefficients from the example calculations. A minus indicates facilitative effects of a competitor. Target species name is given in row, competitor in columns. Ac = *Agrostis capillaris*, Fr = *Festuca rubra*, Hh = *Hydrocotyle heteromeria*, Hl = *Holcus lanatus*, Pv = *Prunella vulgaris*, Rr = *Ranunculus repens*, Tr = *Trifolium repens*.

	Ac	Fr	Hh	Hl	Pv	Rr	Tr
Ac	1	2.044	2.293	1.069	1.612	1.467	0.554
Fr	0.524	1	1.406	0.485	0.755	0.67	0.287
Hh	0.283	0.541	1	0.283	0.502	0.484	0.257
Hl	1.229	1.155	2.517	1	1.33	1.904	0.666
Pv	0.628	1.149	2.399	0.61	1	1.22	0.525
Rr	0.254	0.345	0.814	0.458	0.652	1	0.44
Tr	0.727	1.122	2.701	0.768	1.353	1.899	1

Table 2. Proportion of feasible and stable sets and subsets in published data (feasible and stable sets / number of sets of that size). Stability analysis took place on the competition matrix alone, and may hence be lower still. The Aarssen-data can be compared to the assessment by Wilson and Roxburgh (1992), and the signs '>' and '=' indicate a higher and equal level of stability in their analysis. Data sets for 1977, 1958 and 1939 are from Aarssen (1988). RW refers to Roxburgh and Wilson (2000a).

	Number of species in set					
	7	6	5	4	3	2
Aarssen 1977				0 (0/1) =	0.25 (1/4) =	0.5 (3/6) >
Aarssen 1958				0 (0/1) =	0 (0/4) >	0 (0/6) >
Aarssen 1939				0 (0/1) >	0 (0/4) >	0.33 (2/6) >
RW	0 (0/1)	0 (0/7)	0 (0/21)	0 (0/35)	0.21 (7/34)	0.86 (18/21)

stability ($0.29 + 0.39 = 68\%$ vs $0.39 + 0.14 = 53\%$). The same holds true for the Roxburgh and Wilson (2000a) data, although in all but the three-species sets, feasibility and stability evaluation swing the same direction. In the case of Dormann (2007), all two-species mixtures were reported to be stable, while the three species mixture under unfertilised conditions was neither stable nor feasible. Under fertilisation this changed surprisingly to a feasible and stable coexistence, probably due to a facilitation mechanism that becomes important in one of the fertiliser-sensitive plants.

Higher-order effects, spatial arrangement, zone of influence and other real-world issues

Since many years, theoretical ecologists have been aware of indirect effects in multi-species communities (Levine 1976, Pomerantz 1981, Worthen and Moore 1991, Billick and Case 1994, Wootton 1994, Beckerman et al. 1997). They can be captured by the idea that 'my enemy's enemy is my friend'. Thus even in communities where all pairwise competition coefficients are positive, a third species may have beneficial effects. This can be analysed using the 'inverse method' (Stone and Roberts 1991). They found that the proportion of positive indirect effects can easily reach 40% of all interactions. Nevertheless, these 'higher-order effects' (Case and Bender 1981) are emergent properties of the Lotka–Volterra equations, and are also implicitly included in the stability analysis presented here. While we may argue about the appropriateness of the Lotka–Volterra approach (Wilson et al. 2003), higher-order interactions are no argument against this approach, and hence against the presented application of community matrix theory in plant ecology.

What is the value of analysing competition matrices for our understanding of the relation between competition and coexistence? Until we have not done these analyses, we will not know. Already now, however, we are aware that this approach is rather artificial. We are rarely able to include all species of the community in an experiment due to logistical constraints. Therefore the presence of any

equalising effect of rare species will remain undetected. Furthermore, species-rich systems are not amenable to this approach, again for logistic reasons. And finally, spatial arrangements of individual plants may matter greatly to stability, especially so in terrestrial systems (Stoll and Prati 2001). While we can imagine competition between all species in a well-mixed phytoplankton culture, this is impossible for grassland or forest. Here, every individual will interact mainly with its imminent neighbours. The zone of influence depends on the size of the individual, its interference characteristics (e.g. is it allelopathic or only a scramble-competitor?), and its indirect effects on the community (e.g. mycorrhizal symbionts or deterred herbivores). All these aspects cannot be easily captured by the community matrix approach (but see López-Gómez and Molina-Meyer 2006, 2007).

Yet, it is difficult to pre-guess how important spatial effects are, if we do not understand how stable a community is predicted to be without their consideration. If we know, from decades of observation, that a community is more or less constant in its species composition, we may like to know if this is an intrinsic property, i.e. solely caused by a well-balanced set of competition intensities, or if some external factor stabilises the community (e.g. frequency-independent grazing, frequency-dependent mowing, temporal competition-free niches, Chesson 2000). Once we have assessed the potential of coexistence of a set of plant species, ignoring all real-world issues, we gain an understanding of how strong these real-world effects are.

There is another argument in favour of community matrix theory in experimental plant ecology. Over the years, theoretical ecology has made huge, but abstract, progress in understanding coexistence, diversity, importance of biotic and abiotic interactions and so forth. This progress has mostly been decoupled from experimental studies and experiment-based expertise. Community matrix theory provides an area where theoretical and experimental ecologists can come together. Real data can be used to validate mathematical approaches and, if unrepresentative, models have to be adapted to more realistically depict natural processes. One such example is field-of-neighbour models, in which spatial configuration and plant sizes are incorporated to

Table 3. Separating feasibility and stability. Every species set was assessed for feasibility and stability, with feasibility being more often limiting to coexistence than stability. Data sets for 1977, 1958 and 1939 (from Aarssen 1988) were summarised to illustrate this.

Feasibility	0	1	0	1
Stability	0	0	1	1
1977 / 3 species	1	2	0	1
/ 2 species	0	0	3	3
1958 / 3 species	4	0	0	0
/ 2 species	1	2	3	0
1939 / 3 species	3	0	1	0
/ 2 species	1	0	3	2
Set size-weighted means	0.39	0.14	0.29	0.18
Roxburgh and Wilson (2000a)				
6 species sets	7	0	0	0
5 species sets	21	0	0	0
4 species sets	25	2	8	0
3 species sets	8	6	12	7
2 species sets	1	1	1	18
Dormann (2007)				
2 species sets	0	0	0	6
3 species sets	1	0	0	1

model community processes (Berger and Hildenbrandt 2000, Bauer et al. 2004).

Again, although we restricted our example to a Lotka–Volterra-based community matrix, the more we know about our study system, the better we will be able to formulate more accurate mathematical descriptions of plant competition to construct our community matrix.

Outlook

What are the future ‘tasks’ for CMT? One question so far left unanswered is how increasing system productivity (e.g. by fertilisation) affects competition coefficients and hence coexistence probabilities. From experiments we know that diversity is negatively affected by increased nutrient availability, but the exact mechanism is still obscure (Stevens and Carson 1999, Gough et al. 2000). One valuable recent study has used the Lotka–Volterra equation system behind the community matrix to this end, but not CMT itself (Wilson et al. 2003).

Another avenue is to investigate effects of positive plant–plant interactions on stability of communities. Especially in harsh environments (Arctic, alpine meadows), facilitation seems to be a common phenomenon (Callaway and Walker 1997, Callaway and Pugnaire 1999). But do they contribute to stability, or, as ‘my enemy’s friend is my enemy’, will they lead to lower diversity?

A third potentially interesting research project would be to analyse single-species effects in species-rich communities. For example will an invading species lead to an ‘invasional meltdown’ (Simberloff and Von Holle 1999), by destabilising the community? What is the effect of intrinsically rare species, with a low carrying capacity? Is the stability of a community more sensitive to fluctuations in the abundance of strong than to a weak competitor? One could think of looking at sympatric speciation, where a species of the community develops into a new species with slightly altered competitive ability. Taking this one step further, one may ask if, under continued atmospheric nutrient input, communities with species subject to competition-affecting mutations may intrinsically evolve towards higher stability and diversity, as proposed by Leigh and Vermeij (2002).

Thus, while community matrix theory has its limitations, it also has its merits. Using the latter without ignoring the former may well lead ecologists to increased mechanistic understanding of competitive communities.

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References

- Aarssen, L. W. 1988. 'Pecking order' of four plant species from pastures of different ages. – *Oikos* 51: 3–12.
- Bauer, S. et al. 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.
- Beckerman, A. P. et al. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food web. – *Proc. Natl Acad. Sci. USA* 94: 10735–10738.
- Berger, U. and Hildenbrandt, H. 2000. A new approach to spatially explicit modelling of forest dynamics: spacing, ageing and neighbourhood competition of mangrove trees. – *Ecol. Modell.* 132: 287–302.
- Billick, I. and Case, T. J. 1994. Higher-order interactions in ecological communities – what are they and how can they be detected. – *Ecology* 75: 1529–1543.
- Callaway, R. M. and Pugnaire, F. I. 1999. Facilitation in plant communities. – In: Pugnaire, F. I. and Valladares, F. (eds), *Handbook of functional plant ecology*. Marcel Dekker, pp. 623–648.
- Callaway, R. M. and Walker, L. R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. – *Ecology* 78: 1958–1965.
- Case, T. J. 2000. *An illustrated guide to theoretical ecology*. – Oxford Univ. Press.
- Case, T. J. and Bender, E. A. 1981. Testing for higher-order interactions. – *Am. Nat.* 118: 920–929.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Ann. Rev. Ecol. Syst.* 31: 343–366.
- Ciarlet, P. G. 1985. Introduction à l'analyse numérique matricielle et à l'optimization. – Masson, Paris.
- Damgaard, C. 1998. Plant competition experiments: testing hypotheses and estimating the probability of coexistence. – *Ecology* 79: 1760–1767.
- Dormann, C. F. 2007. Competition hierarchy, transitivity and additivity: investigating the effect of fertilisation on plant-plant interactions using three common bryophytes. – *Plant Ecol.* 191: 171–184.
- Dormann, C. F. and Roxburgh, S. H. 2005. Experimental evidence rejects classical modelling approach to coexistence in plant communities. – *Proc. R. Soc. Lond. B* 272: 1279–1285.
- Firbank, L. G. and Watkinson, A. R. 1985. On the analysis of competition within two-species mixtures of plants. – *J. Appl. Ecol.* 22: 503–517.
- Gough, L. et al. 2000. Fertilization effects on species density and primary productivity in herbaceous plant communities. – *Oikos* 89: 428–439.
- Grime, J. P. et al. 1988. *Comparative plant ecology*. – Hyman, London.
- Istock, C. A. 1977. Logistic interaction of natural populations of two species of waterboatmen. – *Am. Nat.* 111: 279–287.
- Johannsson, M. E. and Keddy, P. A. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. – *Oikos* 60: 27–34.
- Kokkoris, G. D. et al. 1999. Patterns of species interaction strength in assembled theoretical competition communities. – *Ecol. Lett.* 2: 70–74.
- Kokkoris, G. D. et al. 2002. Variability in interaction strength and implications for biodiversity. – *J. Anim. Ecol.* 71: 362–371.
- Leigh, E. G. and Vermeij, G. J. 2002. Does natural selection organize ecosystems for the maintenance of high productivity and diversity? – *Phil. Trans. R. Soc. Lond. B* 357: 709–718.
- Levine, S. H. 1976. Competitive interactions in ecosystems. – *Am. Nat.* 110: 903–910.
- Levins, R. 1968. *Evolution in changing environments*. – Princeton Univ. Press.
- López-Gómez, J. and Molina-Meyer, M. 2006. The competitive exclusion principle versus biodiversity through competitive segregation and further adaptation to spatial heterogeneities. – *Theor. Pop. Biol.* 69: 94–109.
- López-Gómez, J. and Molina-Meyer, M. 2007. Biodiversity through co-opetition. – *Discr. Cont. Dynam. Syst. B* 8: 187–205.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. – Princeton Univ. Press.
- Pimm, S. L. 1982. *Food webs*. – Chicago Univ. Press.
- Pomerantz, M. J. 1981. Do higher-order interactions in competition systems really exist? – *Am. Nat.* 117: 583–591.
- R Development Core Team. 2008. R: a language and environment for statistical computing. – R Found. Stat. Comput., Vienna, Austria, <<http://www.R-project.org>>.
- Roxburgh, S. H. 1994. Estimation of the parameters of the community matrix and implications for community stability using a lawn community. – Bot. Dept, Univ. of Otago.
- Roxburgh, S. H. and Wilson, J. B. 2000a. Stability and coexistence in a lawn community: experimental assessment of the stability of the actual community. – *Oikos* 88: 409–423.
- Roxburgh, S. H. and Wilson, J. B. 2000b. 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.
- Schmitz, O. J. 1997. Press perturbations and the predictability of ecological interactions in a food web. – *Ecology* 78: 55–69.
- Simberloff, D. and Von Holle, B. 1999. Positive interactions of non-indigenous species: invasional meltdown? – *Biol. Invas.* 1: 21–32.
- Stevens, M. H. H. and Carson, W. P. 1999. Plant density determines species richness along an experimental fertility gradient. – *Ecology* 80: 455–465.
- Stoll, P. and Prati, D. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. – *Ecology* 82: 319–327.
- Stone, L. and Roberts, A. 1991. Conditions for a species to gain advantage from the presence of competitors. – *Ecology* 72: 1964–1972.
- Wilson, J. B. and Roxburgh, S. H. 1992. Application of community matrix theory to plant competition. – *Oikos* 65: 343–348.
- Wilson, W. G. et al. 2003. Biodiversity and species interactions: extending Lotka–Volterra community theory. – *Ecol. Lett.* 6: 944–952.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. – *Ann. Rev. Ecol. Syst.* 25: 443–466.
- Worthen, W. B. and Moore, J. L. 1991. Higher-order interactions and indirect effects: a resolution using laboratory *Drosophila* communities. – *Am. Nat.* 138: 1092–1104.