# Stability and coexistence in a lawn community: mathematical prediction of stability using a community matrix with parameters derived from competition experiments

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Community matrix theory has been proposed as a means of predicting whether a particular set of species will form a stable mixture. However, the approach has rarely been used with data from real communities. Using plant competition experiments, we use community matrix theory to predict the stability and competitive structuring of a lawn community.

Seven species from the lawn, including the six most abundant, were grown in boxes, in conditions very similar to those on the lawn. They were grown alone (monocultures), and in all possible pairs.

The species formed a transitive hierarchy of competitive ability, with most pairs of species showing asymmetric competition. Relative competitive ability (competitive effect) was positively correlated with published estimates of the maximum relative growth rate ( $RGR_{max}$ ) for the same species.

A seven-species community matrix predicted the mixture of species to be unstable. Simulations revealed two topological features of this community matrix. First, the matrix was closer to the stability/instability boundary than predicted from a range of null (random) models, suggesting that the lawn may be close to stability. Second, the tendencies of the lawn species to compete asymmetrically, and to be arranged in competitive hierarchies, were found to be positively associated with stability, and hence may be contributing factors to the near-stability seen in the matrix.

The limitations of using competition experiments for constructing community matrices are discussed.

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Perhaps the most crucial question in community ecology is whether communities are self-regulating, to the extent that they can recover their state after a perturbation, i.e. whether they are stable (Pimm 1984). Moreover, the question most commonly asked when ecologists are consulted is whether a particular community is stable, and therefore whether a particular planned land management is likely to have a lasting effect on the community (Peterman 1980). May (1972) initiated the modern approach to stability, with his community matrix analysis. This is based on a mathematical procedure called local stability analysis (= 'Liapunov stability analysis' = 'neighbourhood stability analysis'). In ecological terms, the community matrix summarises all possible pairwise species interactions in an equilibrium community. The stability of a community, i.e. whether a mixture of species that are coexisting at equilibrium will return to that equilibrium

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following perturbation, can be predicted mathematically from the community matrix.

Since May's (1972) analysis, the community matrix has been used extensively in theoretical studies to predict the patterns of interactions among species that would be expected to result in the persistence of multispecies mixtures in nature. Particular emphasis has been placed on investigating the relationship between the complexity of ecological systems and stability (for reviews see Pimm 1982, 1984, Lawton 1989, Hall and Raffaelli 1993).

To briefly summarise the results from this vast literature, given a matrix comprising random values, communities with many species and/or with many or strong interspecific interactions are less likely to be stable. In fact, it is very unlikely that a community of randomly assembled species will be stable at all. This represents an obvious conflict with the observation that multispecies communities commonly persist in nature. One explanation is that the species in natural communities have co-evolved to be able to co-exist stably. However, it has been found that the introduction of some basic ecological processes, especially simulating the assembly of a community by the immigration and extinction of species, allows complex multispecies communities to develop relatively easily (Taylor 1988, Haydon 1994).

Despite the dominant role that the community matrix has played in the development of theory relating to the stability and persistence of ecological communities, almost all of the extensive literature on the community matrix has dealt with theoretically constructed matrices. Progress in testing predictions of the theory using natural systems has been surprisingly slow. Most such tests have been clouded by uncertainty over the validity of the data. For example it has been suggested that studies based on the analysis of food webs (e.g. Briand 1983, Auerbach 1984) are unreliable due to biases in the data (Paine 1988, Kenny and Loehle 1991). Another approach has been to estimate the community matrix by using the observed distributions of organisms (Mc-Naughton 1978, Gitay and Agnew 1989, Hallett 1991), but it has been pointed out that it is impossible to estimate species interactions from association data alone (Hastings 1987, Keddy 1989, but see Wilson and Gitay 1995).

The only valid method for estimating the community matrix for a given community is by the experimental manipulation of the organisms, quantifying the effect that each species has upon the growth rate of each species. We are aware of only four studies which have used this approach in the investigation of community stability (Seifert and Seifert 1976, Thomas and Pomerantz 1981, Wilson and Roxburgh 1992, Schmitz 1997). Never has the stability of a community been estimated using the community matrix, and that prediction of stability then been tested in the field. We set out to do this for the first time. Because there has been so little empirical testing of the community matrix, two crucial questions remain open: a. whether communities in the field are usually stable, and b. whether stability can, as May suggested, be predicted from the values of the community matrix.

We tested the ability of community matrix theory to predict stability in a community of herbaceous lawn plants. In this paper, we describe how a community matrix for the lawn was estimated, and was used to make predictions of how the vegetation would respond to perturbation. In a companion paper these predictions are tested through experimental manipulation of the community (Roxburgh and Wilson 2000).

To assist the reader, we first provide an introduction to the theory.

# Introduction to community matrix theory

#### **Interaction equations**

Consider a community of organisms co-occurring in some spatially well-defined area, such as a lawn community comprising n species of plants. If each of these n species is increasing (or decreasing) over time in response to changes in the abundance (density or biomass) of other species, the population growth rate of each species may by described by n equations with the very general form:

$$\frac{dN_i}{dt} = f_i(N_1, N_2, \dots, N_n) \quad i = 1, 2, \dots, n.$$
(1)

These equations simply state that, for a species *i*, the rate of change in its abundance  $(dN_i/dt)$  is some function of both interspecific and intraspecific interactions. In the vast majority of theoretical studies, the actual interaction equations used have been Lotka-Volterra competition equations, where the per capita growth rate is a linear function of the  $N_i$  values (Pimm 1982, Hall and Raffaelli 1993). Note that abiotic factors are included only indirectly through their effects on the species abundances. The implications of this aspect of the theory, and in particular the potential importance of environmental fluctuations on species coexistence, are considered in greater detail in the section 'Mechanisms of species coexistence', and in the companion paper (Roxburgh and Wilson 2000).

#### Equilibrium

To determine the stability of a community, it must first be assumed that the mixture has reached equilibrium. Equilibrium is the state in which the rate of recruitment of new individuals (or biomass) for each species is equivalent to the rate of death, so for all species the total net change over time is zero. In the lawn, this would be observed as lack of change in the abundances of the n plant species over time. Mathematically this can be expressed as

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = 0 = f_i(\hat{N}_1, \hat{N}_2, \dots, \hat{N}_n) \quad i = 1, 2, \dots, n,$$
(2)

where  $\hat{N}_i$  are the equilibrium abundances for each species, and are found by equating Eq. 1 to zero.

Mathematically, an equilibrium can occur with some or all of the species at negative abundances. Such an equilibrium has no biological meaning, and is called 'unfeasible' (Roberts 1974). Similarly, the equilibrium abundance of some or all of the species can be zero, and such solutions are called 'trivial'.

### Stability

In general, the non-linear Eq. 1 cannot be solved explicitly, but in the region of the equilibrium (as defined by Eq. 2), which is the region of relevance for determination of stability, it can be approximated by linear equations. These linear approximations can then be solved and used to investigate the stability of the community in the region of the equilibrium, i.e. whether all the species would be expected to recover following a small perturbation. The first step is to perturb the abundance of each species by a small amount  $x_i$  away from equilibrium. Formally

$$x_i = N'_i - \hat{N}_i$$
  $i = 1, 2, \dots, n,$  (3)

where  $N'_i$  is the density of species *i* after a displacement of  $x_i$  from the equilibrium  $\hat{N}_i$ . Then, changes in the  $x_i$ are followed through time. If each species eventually returns to its original abundance, however long it takes, then the community as a whole has recovered and is therefore locally stable. If at least one species remains different from its original abundance, the community is said to be unstable.

For brevity we will skip over the mathematical steps required to derive an expression which describes how the  $x_i$  change with time (for a full treatment see Pimm 1982), and jump straight to the 'community matrix', which we will denote by the symbol **S**. In a community of *n* species, the community matrix is an  $n \times n$  matrix with elements:

$$s_{ij} = \left(\frac{\partial f_i}{\partial N_j}\right)^*,\tag{4}$$

where  $s_{ij}$  quantifies the effect that perturbing species 'j' from equilibrium by the small amount ' $\partial N_j$ ' has on the growth of species 'i', given by ' $\partial f_i$ '. The  $s_{ii}$  elements represent intraspecific interactions, and the  $s_{ij}$  elements

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represent interspecific interactions. To determine local stability, we calculate the *n* eigenvalues of the community matrix. If all of the eigenvalues are less than zero, then following perturbation, all the species will return to their pre-perturbation equilibrium abundances, i.e. the community is stable. All we need, therefore, is  $R(\lambda)_{\text{max}}$ , the real part of the largest eigenvalue. A negative value of  $R(\lambda)_{\text{max}}$  indicates community stability, and a positive value indicates instability.

#### Application of community matrix theory

In using community matrix theory to predict stability in the real world, four assumptions must be met: (1) equilibrium, (2) small perturbations, (3) instantaneous perturbations, and (4) spatial homogeneity.

#### **Assumption 1: Equilibrium**

The stability predictions are valid only if the community is at equilibrium. In the strict mathematical sense a community is at equilibrium only when the rate of change for all species is zero (Eq. 2). This assumption is often seen as the major limitation of the theory, simply because this theoretical ideal could never be achieved in natural communities, e.g. due to seasonal and stochastic environmental variation (Wiens 1984). However, despite this limitation, both theoretical and empirical investigators have attempted to use the theory as a tool for predicting or investigating the dynamics of real communities.

In applying the theory to real communities the question becomes not whether the species are coexisting at the ideal of a point equilibrium (because the answer will always be 'no'), but rather how far the community is from the ideal, and what effect that has on the validity of predictions based on the theory. To date, there have been no empirical studies which have simultaneously aimed to both apply community matrix theory and also investigate in detail the assumption of equilibrium. Because our aim was to provide a thorough application of the theory, we set out to do this for the first time.

The methods used to test for equilibrium in our study community are described in Roxburgh and Wilson (2000). Our overall conclusion there is that the data are consistent with the existence of an equilibrium over a medium time-scale. However, the presence of betweenseason and between-year variation in the abundances of some of the species indicates departure from the pointequilibrium ideal.

#### **Assumption 2: Small perturbations**

The second limitation is that the analysis predicts only 'local' stability, i.e. stability after arbitrarily small perturbations. Although 'arbitrarily small' perturbations are easily defined mathematically, in a natural system the effects of a very small perturbation will inevitably be swamped by environmental noise. It would be desirable to specify a perturbation within the domain in which the linear approximations are valid, but in natural communities this domain is unknown. Experimentally, one has to apply a perturbation large enough to ensure a measurable effect on the community. If the community recovers, then we can conclude that it is at least locally stable, and may be globally stable. If the community has not recovered, then the perturbation may have been too great to test for local stability, or there has not yet been enough time for recovery to have occurred, or the community is unstable.

### **Assumption 3: Instantaneous perturbations**

The theory assumes that the perturbations are instantaneous. While many natural perturbations may be temporally well-defined, such as episodes of flooding or temporary shading, there are others which may last for very long periods, such as climatic changes and radioactive pollution. These latter perturbations are incompatible with local stability analysis (Kindlmann and Lepš 1986).

## Assumption 4: Spatial homogeneity

Eqs (1) incorporate an implicit assumption of spatial homogeneity. In real communities this can be observed as a lack of spatial structure in the distribution patterns of the species; i.e., for the theory to be validly applied, the species must be well intermixed, to ensure that they all have the opportunity to interact with one another.

#### Where can community matrix theory be applied?

Because of these limitations, a number of authors have suggested that the value of models such as the community matrix lies in their ability to provide inspiration for developing new hypotheses, even though they are too simplistic as 'working models' to apply to real communities (e.g. May 1984). However, as Pimm (1992: xiv) pointed out "What then is the purpose of building ecosystem models if we cannot test them; how do we know the models are not purely theoretical edifices?".

We do not imply in this work that the community matrix model (with its simplistic assumptions) is relevant to all natural communities. It has been argued that many persist in a non-equilibrium state, and that environmental variation plays an integral role in the maintenance of their diversity (e.g. Chesson and Huntly 1989). Here, we attempt to apply community matrix theory to a real community that was chosen as coming as close as possible to satisfying the assumptions – the Otago University Botany lawn. If the usefulness of the theory cannot be demonstrated using this simplest of communities, then the claim that the theory is too simplistic to adequately represent real communities must be taken very seriously, and the validity of results derived from a whole suite of theoretical studies must be questioned. Note that because this study is limited to a single community, we were unable to directly investigate issues related to between-community differences in stability, such as the stability-diversity debate.

### **Experimental methods**

## The Botany lawn study site

The lawn, 13 m  $\times$  11 m, is situated in a secluded part of the Otago University campus, Dunedin, New Zealand, at an altitude of ca 5 m a.s.l. It was established during the early 1960s (Professor G. T. S. Baylis pers. comm.), since when the only management has been regular mowing. The lawn is mown to a constant height, and all clippings are collected in a catcher and removed from the site. During the summer months, mowing frequency averages approximately once every two weeks, and in the winter once every two months. That the lawn is subject to a continuous mowing regime is not incompatible with the concept of equilibrium, since the mowing treatment is a constant and predictable background feature of the environment, and the removal of foliage from the vegetatively reproducing species does not result in the death of entire plants. In this, mowing is comparable with natural herbivory. This can be contrasted with typical 'disequilibrium' processes such as unpredictable disturbances, which open up space and initiate successions in many communities.

We chose a lawn on which to apply community matrix theory because: (1) The species within the mown sward are generally well-mixed and closely-packed, with little or no bare ground; under such conditions competition may be expected to be intense, and thus play a significant rôle in structuring the community. Although mowing removes biomass from the canopy, and is thus potentially reducing competition for light, previous work on this community has shown that the species do compete strongly with each other, even under these conditions (Watkins and Wilson 1992, Wilson et al. 1992, Wilson and Roxburgh 1994). (2) The species that are characteristic of lawns are generally fast growing, so there is potential for a high rate of biomass turnover, and for fast community development; therefore in wellestablished lawns it is more likely that the species in the community have reached equilibrium. (3) Fast growing herbaceous plants are easy to manipulate under experimental conditions.

#### **Experimental rationale**

The elements of the community matrix were determined from pairwise competition experiments, estimating the effect of one species upon another by comparing the performance of each species when grown in mixture, to its performance when grown in monoculture. An additive experimental design was used (Underwood 1986), i.e. the planting density for each species in mixture and in the corresponding monoculture was the same. With an additive design, if species A has no competitive effect on species B, the biomass of species B in mixture and in monoculture will be the same.

To predict stability, a seven-species community matrix, with 49 elements, was constructed. Seven species were chosen from the 23 vascular plant species recorded in the undisturbed lawn (Roxburgh 1994). The number of seven species was a trade-off between the number of species combinations required to estimate the matrix parameters, the number of replicates required to attain satisfactory statistical power, and the physical space available adjacent to the lawn. The seven species together comprised 81% of the total point quadrat hits for the lawn (Roxburgh and Wilson 2000). Six of the species were the most common ones found on the lawn: three grasses (Agrostis capillaris, Holcus lanatus and Festuca rubra) and three forbs (Trifolium repens, Prunella vulgaris and Hydrocotyle heteromeria). The seventh species was Ranunculus repens, one of the rarer species found in the lawn, which was included so that the experimental mixture represented a wider range of field abundances. Note that, because it is not possible to include all species in the experiment, we are making the assumption that the stability properties of the seven-species matrix are consistent with the full matrix. This assumption is discussed in greater detail in the section 'Limitations of the stability analysis'.

#### **Experimental design**

The following 35 types of box were set up:

- a monoculture box for each species, planted with three ramets per box (single-density monoculture),
- a monoculture box for each species, planted with six ramets per box (double-density monoculture),
- all possible (21) two-way mixtures of the seven species, planted with three ramets of each species.

Aarssen (1985) and Taylor and Aarssen (1989) have shown that the results of pairwise competition experiments, as described above, are valid only when it can been shown that both species in monoculture are fully utilising the resource space, i.e. the monocultures achieve constant final yield (CFY). To check for CFY therefore requires confirming that the final (12-month) biomass of the single- and double-density monocultures was the same (Taylor and Aarssen 1989, Johansson and Keddy 1991).

There were ten replicates of each treatment, arranged in a randomised block design, 350 boxes overall. For each species in each block a single clone was used, to control error variation, but also to ensure that each replicate was independent from the moment of collection of the original ramets.

#### Plant and soil materials

Ramets of the seven species were collected at random from the lawn, 13 months before the establishment of the experiments, and cloned. During this period the clones were regularly clipped, mimicking the action of the lawn mower.

The soil used in the boxes was collected from the Botany lawn, from holes 20 cm deep at random positions (away from the perturbation experiment blocks: Roxburgh and Wilson 2000). The top 5 cm of vegetation was discarded. In the remaining soil, the top and bottom halves of the profile were kept separate to retain, in the boxes, a soil structure as close as possible to that in the Botany lawn. The bottom layer was placed, unsterilised but thoroughly mixed, in the bottom of the experimental boxes to allow the introduction of naturally occurring soil organisms. The remaining soil was steam sterilised at 102°C for 3 h to destroy the propagule bank, mixed and placed in the boxes on top of the unsterilised soil.

# Planting, establishment, maintenance and harvesting

The experiment was established in February 1991, ca 20 m from the Botany lawn, in wooden boxes with dimensions  $20 \times 20 \times 20$  cm. In the pairwise mixtures the ramets were planted in a chequerboard pattern, in close proximity to one another, to ensure that the species were given the opportunity to interact at the earliest possible opportunity. For the first two weeks of growth, the boxes were covered with shade cloth to aid establishment. Dead ramets were replaced for up to six weeks with live material of the same genotype (mortality before replacement was 10%). During the experiment, the boxes were clipped by hand to simulate the mowing regime on the lawn. As with the mowing, the clippings were discarded, and were not allowed to decompose in situ. Clipping frequency mirrored that of the lawn mowing: every two weeks in summer and every two months in winter.

All boxes were harvested exactly 12 months after they were set up, having been clipped two weeks before that date. At harvest, the above-ground vegetation of the boxes was removed, sorted into species, dried and weighed. Because we wanted the conditions in the competition experiment to be as close as possible to those in the actual community, we did not alter the natural soil matrix, e.g. by mixing sand. Unfortunately, this meant we were unable to harvest the below-ground biomass, due to difficulty in separating root material from the soil, and difficulty in disentangling the roots of competitors.

## Stability analysis methods

To predict stability the results of the pairwise competition experiments were first expressed as the 'Relative Yield per Plant', RYP, which for the additive design is defined as:

$$\mathbf{RYP}_{ij} = \frac{Y_{ij}}{Y_i},$$

where  $Y_{ij}$  is the yield from three ramets of species *i* after competing with three ramets of species *j* and  $Y_i$  is the single-density monoculture yield of three ramets of species *i*. For interspecific competition  $i \neq j$  and for intraspecific competition i = j. RYP values were calculated for each replicate (i.e. block) separately to allow calculation of the variance of the RYP values.

To calculate the elements of the community matrix from the RYP values the method of Wilson and Roxburgh (1992) was used. A summary of that method follows.

The interpretation of matrix elements  $s_{ii}$  (Eq. 4) is that, in a mixture near equilibrium, changing the abundance of species j by the small amount  $\partial N_i$  will have an effect on species *i* of  $\partial f_i$ . The ratio effect:change gives  $s_{ii}$ . If, when extra plants of *i* are added to a box, growth of other plants is reduced to exactly compensate (as in a monoculture at CFY, when the plants have reached environmental carrying capacity), RYP will be 0.5 and  $s_{ii}$  or  $s_{ii}$  will be -1.0. If there is no interaction between plants/species, RYP will be 1.0 and  $s_{ii}$  or  $s_{ii}$  will be 0.0. If there is exact mutualism (i.e. adding extra plants to the box results in an increase in the growth of the existing plants to exactly match), RYP will be 2.0 and  $s_{ii}$  or  $s_{ii}$  will be + 1.0. Therefore, to convert RYP values into  $s_{ii}$  community matrix elements we apply the transformation:

$$s_{ij} = \log_2(\text{RYP}_{ij}). \tag{5}$$

The appropriate form of the transformation in between RYP values of 0.5, 1.0 and 2.0 is unknown, but the assumption is that the transformed RYP values are approximations to the elements of the community matrix, or are related in such a way that the stability properties of the transformed RYP matrix parallel those of the 'actual but unknown' community matrix. Stability is determined from **S** as described in the Introduction, calculating the maximum eigenvalue  $R(\lambda)_{max}$  (by algorithm HQR; Press et al. 1986).

Table 1. Matrix of average RYP values and standard deviations (in parentheses) from the pairwise competition experiments (n = 10 replicates). Column (effect) and row (response) averages are calculated with the diagonal elements excluded. Effect and response values sharing the same letter are not significantly different (Tukey's test, P = 0.05). \* = RYP values not significantly different from 1.0 by *t*-test (P = 0.05). Species abbreviations: HI = Holcus lanatus, Ac = Agrostis capillaris, Rr = Ranunculus repens, Tr = Trifolium repens, Fr = Festuca rubra, Pv = Prunella vulgaris, HI = Hydrocotyle heteromeria.

Target species	Neighbour species							Mean response
	Hl	Ac	Rr	Tr	Fr	Pv	Hh	_
Hl	0.52 (0.12)	0.75 (0.28)	0.60 (0.33)	0.65 (0.21)	$1.00^{*}$	0.99*	0.98*	0.83a (0.23)
Ac	0.27	0.53	0.46	0.73 (0.20)	0.77 (0.27)	$0.88^{*}$	$0.97^{*}$	$0.68^{ab}$ (0.33)
Rr	0.48	0.74	0.49	0.37 (0.12)	0.83	0.82	0.86	$0.68^{ab}$ (0.25)
Tr	0.56	0.58	0.70	0.52	0.70 (0.14)	0.68	0.82	(0.23) $0.67^{ab}$ (0.12)
Fr	0.12	0.29	0.49	0.63	0.53	0.65	0.87	(0.12) $0.51^{abc}$ (0.23)
Pv	(0.03) 0.11 (0.07)	(0.21) 0.17 (0.08)	(0.27) 0.23 (0.09)	0.45	(0.09) 0.43 (0.18)	(0.29) 0.50 (0.13)	0.63 (0.24)	(0.33) $0.34^{bc}$ (0.25)
Hh	0.11	0.11	0.31	0.27	0.22	0.34	0.51	$(0.23)^{\circ}$ $(0.13)^{\circ}$
Mean effect	(0.00) $0.27^{a}$ (0.25)	(0.00) $0.44^{ab}$ (0.35)	(0.10) $0.46^{abc}$ (0.21)	(0.11) $0.52^{abc}$ (0.22)	(0.12) $0.66^{abc}$ (0.35)	(0.19) $0.73^{bc}$ (0.28)	(0.10) $0.85^{\circ}$ (0.15)	(0.15)

Table 2. Matrix of *P* values from *t*-tests between pairwise competitors (see Table 1). Statistically significant *P* values are indicated in bold (P = 0.05), and indicate that the row species is competitively superior to the column species. \* indicates *t*-tests based on log-transformed values to homogenise unequal variances.

	Holcus	Agrostis	Trifolium	Ranunculus	Festuca	Prunella	Hydrocotyle
	lanatus	capillaris	repens	repens	rubra	vulgaris	heteromeria
H. lanatus A. capillaris T. repens R. repens F. rubra P. vulgaris		0.000 0.009	0.386* 0.078	0.422 0.000	0.000* 0.001* 0.316 0.008	0.000* 0.000* 0.002 0.000* 0.077	0.000* 0.000* 0.000 0.000 0.000 0.000 0.010

#### **Results and discussion**

#### Patterns of competition

#### Interspecific competition

All of the interspecific RYP values except five (Table 1) were significantly < 1.0 (based on pairwise *t*-tests, P < 0.05), i.e. suppression in mixture relative to monoculture was detected in 37/42 of the possible combinations.

#### Intraspecific competition

None of the diagonal RYP elements were significantly different from 0.5. This means that comparison between the single- and double-density monocultures gave no evidence for unused resources in the single-density monocultures, suggesting that after 12 months' growth constant final yield had been attained (Aarssen 1985, Taylor and Aarssen 1989).

#### Effect/response, and asymmetry

Competitive interactions in multispecies communities can be separated into two processes: the effect that a species has on all others in the community, and the response of a species to all others (Miller and Werner 1987). The overall effect and response (Table 1) are seen as the row and column averages, excluding the diagonal elements. The mean effect ranged from 0.27 for *Holcus lanatus* (indicating that on average *Holcus* depressed the performance of other species to 27% of that which they attained in monoculture) to 0.85 for *Hydrocotyle heteromeria*. Tukey's range test indicated that there was a continuous variation in competitive effect, from *Holcus*, the most competitive species, to *Hydrocotyle*, the weakest.

Competitive response values ranged from 0.83 for *Holcus* (indicating that on average other species decreased the performance of *Holcus* to 83% of its performance in monoculture) to 0.23 for *Hydrocotyle*. Tukey's test again showed continuous variation between these two extremes. This continuum of competitive ability is in contrast to the results of Johansson and Keddy (1991), where the species clearly split into three superior competitors and three inferior competitors. Competitive effect and response were significantly negatively correlated across species (r = -0.978, P < 0.001), illustrating that there was usually asymmetric pairwise

competition between the species pairs, with a 'winner' and a 'loser', as Miller and Werner (1987) found for five herbaceous old-field species, and Johansson and Keddy (1991) for 'wetland' species.

The extent of the competitive asymmetry was investigated further by performing *t*-tests between each pair of RYP values. Of the 21 pairwise comparisons, 16 showed significant difference (Table 2) between reciprocal RYP values (Table 1), i.e. asymmetry in competition, i.e. a greater competitive ability for one species of the pair.

#### *Hierarchy and transitivity*

The pattern of the asymmetric competitive relations among the seven species shown in Table 2 was such



Fig. 1. Hierarchy of competitive abilities based on the results of the pairwise competition experiment. An arrow leaving species A and terminating at species B indicates that species A suppressed B significantly more strongly than species B suppressed A, as defined by the *t*-tests in Table 2.



Fig. 2. Competitive effect from Table 1 vs maximum relative growth (RGR) as measured by Grime and Hunt (1975) for six of the seven species used in the competition experiments (all except *Hydrocotyle heteromeria*). Note the inverted x-axis. See Table 1 for species abbreviations.

that they could be arranged into a linear hierarchy of competitive ability (Fig. 1), the most competitive at the top (*Holcus lanatus*, competitively superior to four species and inferior to none) to the least competitive at the bottom (*Hydrocotyle heteromeria*, competitively inferior to six species and superior to none). This linear hierarchy (i.e. transitivity of competitive ability: Keddy and Shipley 1989) supports the conclusion of Miller and Werner (1987), that in many plant communities there is little specificity of species interactions, e.g. the most dominant species affects all other species strongly, not just some of them. The latter workers interpreted this as evidence that all the species are competing for the same resources, i.e. light, water and nutrients. Transitive competitive hierarchies have been found to be a feature of many competition studies of herbaceous plant communities (Shipley 1993).

Gaudet and Keddy (1988) proposed that the competitive abilities of species, e.g. their position in a competitive hierarchy, might be predicted from a small number of species-specific traits. In particular they argued that plant size, together with related morphological characters, has the potential to predict the outcomes of plant competition experiments. We suggest that for the Botany lawn species plant size per se is irrelevant, due to the constant mowing regime. However, the competitive effects of the species (i.e. their ability to suppress neighbours; Table 1) were related to their maximum relative growth rates (RGR<sub>max</sub>; Fig. 2) as determined by Grime and Hunt (1975). This strong relation ( $r^2 =$ 0.897, P = 0.004), although based on only six species, supports Gaudet and Keddy's (1988) claim that competitive ability might be predictable from a small number of traits.

### Stability analysis

Each element in the observed RYP matrix (Table 1) has an uncertainty associated with its estimation, measured as a standard deviation. To generate an estimated community matrix incorporating this uncertainty, community matrix elements were drawn at random from a normal distribution with mean and standard deviation equal to that in the observed RYP matrix. For each 'resampled' RYP matrix, the transformation of Wilson and Roxburgh (1992) was used to convert it to a community matrix. 1000 such matrices were generated. The average matrix and its standard deviation over these 1000 estimates is shown in Table 3.

Eigenvalue analysis of the estimated community matrix predicted instability of the mixture, with a maximum eigenvalue  $R(\lambda)_{\text{max}} = 0.019$ . This suggests that the Botany lawn is unstable, and therefore will not recover

Table 3. Estimated community matrix for the Botany lawn calculated from 1000 community matrices randomly generated from the RYP values in Table 1. Values in parentheses are standard deviations. See text for further details.

Target species	Neighbour species								
	Hl	Ac	Rr	Tr	Fr	Pv	Hh		
Hl	-0.94	-0.41	-0.76	-0.63	0.01	-0.02	-0.03		
Ac	(0.04) -1.90 (0.14)	-0.92	-1.12	-0.45	-0.39 (0.14)	-0.18	(0.10) -0.04 (0.09)		
Rr	-1.06 (0.20)	-0.43 (0.12)	-1.04 (0.02)	-1.44 (0.06)	-0.28 (0.08)	-0.30 (0.07)	-0.23 (0.03)		
Tr	-0.84 (0.02)	-0.79 (0.05)	-0.52 (0.02)	-0.94 (0.01)	-0.51 (0.04)	-0.55 (0.03)	-0.29 (0.04)		
Fr	-3.10 (0.03)	-1.78 (0.23)	-1.05 (0.21)	-0.68 (0.07)	-0.91 (0.02)	-0.64 (0.20)	-0.21 (0.04)		
Pv	-3.21 (0.06)	-2.55 (0.05)	-2.15 (0.05)	-1.17 (0.08)	-1.22 (0.10)	-0.99 (0.05)	-0.67 (0.13)		
Hh	-3.25 (0.05)	-3.21 (0.05)	-1.69 (0.12)	-1.88 (0.07)	-2.22 (0.10)	-1.54 (0.15)	-0.98 (0.03)		

following perturbation. It interesting to note that 0.019 appears close to the stability/instability boundary of 0.0, and also that the 95% quantile of eigenvalues for the 1000 community matrices from which the average matrix was calculated includes zero (-0.005, 0.465). These observations suggest the possibility that the observed community matrix may be close to the boundary of stability/instability, implying that the community itself is close to being stable. This would be an ecologically interesting result, and for this reason we chose to examine the topology of this community matrix in greater detail.

# Statistical explorations of the observed community matrix

To gain a deeper appreciation of the topological characteristics of the community matrix, we used a null models approach. We noted above that the estimated value of  $R(\lambda)_{max}$  appears close to the stability/instability boundary value of 0.0. However, to make conclusions about how 'close' or 'far' the community is from this boundary requires comparison with an appropriate null model. This is a problem, because it is difficult to know how much ecological information the null model should include. We therefore used four different null models, with characteristics which represent different aspects of the observed interspecific interactions. The procedure is similar to that used by Lawlor (1980) in his analysis of 11 lizard and 10 bird community matrices.

For each null model, 5000 seven-species community matrices were constructed,  $R(\lambda)_{max}$  for each random matrix was recorded, and the observed value was compared with the frequency distribution of the null model values. The four null models are as follows:

1. Random values. In the observed RYP matrix, the off-diagonal elements ranged from 0.11 to 1.00, with the distribution approximately rectangular. The 'Random values' algorithm constructed RYP matrices by filling the off-diagonal cells from a rectangular-random distribution with the same range. The diagonal elements were assigned the average of the value of the observed matrix (= 0.51). These random RYP matrices were then converted to community matrices by Eq. 5, and their stability determined. (Random RYP matrices were generated here, rather than random community matrices directly, as the distribution of the observed RYP values was closer to a rectangular than the distribution of the community matrix elements.) This model retains a minimum amount of the original community structure, in that there is no constraint on the patterns of interactions among the species.

2. Random positions. For this algorithm, the off-diagonal  $s_{ij}$  values in the observed community matrix were retained, but they were allocated to positions at ran-

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dom. Since this model retains in the random matrices only the observed values, not their positions, it tests what effect the arrangement of the observed elements has on community stability. The values of the observed diagonal elements were also retained, but allocated at random along the diagonal.

3. Random pairs. This algorithm also retains the observed  $s_{ij}$  values, but in addition it retains the observed 'asymmetric' pairwise competitive relationships, by keeping the 21  $s_{ij}/s_{ji}$  competitive pairs as pairs, and randomly allocating those pairs. The orientation of each pair above/below the diagonal was randomised, to disrupt the observed tendency of the species to form a transitive competitive hierarchy.

4. Random pairs and hierarchy retained. The only difference between this algorithm and the previous model was that the tendency for the species to be arranged into competitive hierarchies was retained in the random matrices, by retaining the observed above/below diagonal orientation of the competitive pairs. This algorithm produces random matrices which are topologically very similar to the observed community matrix.

The null model analysis provides two sorts of information. First, it gives an indication of how likely it is to observe a stable seven-species matrix at random, under a variety of constraints. (results presented below under 'Analysis 1'). Second, it provides an indication of where the observed matrix occurs relative to the distribution of matrices generated from a particular null model. The closeness of the observed matrix to the stability/instability boundary can be quantified by counting the number of random matrices that had  $R(\lambda)_{max}$  values less than the observed matrix, but greater than zero. If this number is very small, then this indicates that the observed matrix is indeed close to the boundary (results presented below under 'Analysis 2'). Two further aspects of the topology of this matrix were investigated. In the third analysis we explore the stability properties of subsets of species within the matrix (Analysis 3). In the fourth we investigate how sensitive the prediction of instability is to changes in the above/below diagonal structure of the matrix, i.e. diagonal dominance. This is a characteristic that is critical in determining community stability (Analysis 4).

# Analysis 1: Probability of stability under the null models

Under the Random values null model there was a very low chance of observing a stable seven-species matrix, with only 1/5000 matrices having a  $R(\lambda)_{max}$  value of less than zero (Fig. 3a). Through models 2–4, as the similarity of the null model to the observed matrix increased, the chance of observing a stable seven-species matrix increased correspondingly. In particular with



Fig. 3. Frequency histograms of  $R(\lambda)_{max}$  calculated from 5000 randomly generated matrices for each of four null models. The arrow indicates the interval containing  $R(\lambda)_{max}$  for the community matrix calculated for the Botany lawn. Open bars indicate stable communities, i.e. matrices with  $R(\lambda)_{max} < 0$ . See text for further details.

model 4 (Fig. 3d), which retains both the observed competitive asymmetry and competitive hierarchies, the chance of observing a stable matrix increased to 630/5000, or 13%. This suggests that competitive asymmetry and competitive hierarchies enhance the chance of forming a stable mixture. Strong pairwise competitive asymmetry and competitive hierarchies are consistent with at least one model of multispecies coexistence, described by Keddy (1989) as the 'competitive hierarchy' model.

Asymmetric competition appears to be common in plant communities (Connell 1983, Schoener 1983), and Shipley (1993) has further suggested that the tendency to form competitive hierarchies is a common feature of many herbaceous plant communities (but see Connolly 1997). Although the link between competitive asymmetry and stability has been suggested by previous theoretical studies (Rummel and Roughgarden 1985, Ginzburg et al. 1988), Fig. 3 represents the first time that both asymmetry and competitive hierarchies have been directly linked to a model of community dynamics.

Lawlor (1980), analysing 11 lizard communities and 10 bird communities using a null model very similar to the Random positions, found observed matrices to exhibit 'higher stability' than the corresponding random communities, although it should be noted that Lawlor's 'community matrices' were actually matrices of overlap indices, and are approximations to matrices of Lotka-Volterra competition coefficients rather than to the community matrix **S**.

#### Analysis 2: Closeness of the observed community matrix to the stability/instability boundary

In Fig. 3 it can be seen that, under all null models, the value of  $R(\lambda)_{max}$  for the Botany lawn matrix was

extremely close to the stability/instability boundary value of 0.0. This closeness is confirmed when the number of random matrices greater than 0.0 but less than the observed matrix are counted. For both the Random values and Random positions models, there were no random matrices with a value of  $R(\lambda)_{max}$  in this interval. For the Random pairs model, only 20/5000 or 0.4% of the random matrices were closer to the boundary than the observed matrix, and for model 4 this increased to just 4.3%. These results confirm that the Botany lawn community matrix is extremely close to the boundary of stability/instability, at least when compared against the range of null models considered. This is an interesting result, in that it predicts a community which may be 'teetering' on the edge of stability. That the observed matrix is close to the stability/instability boundary can also been seen by the sensitivity of the stability predictions to minor changes in the diagonal vs off diagonal structure of the matrix, described below under Analysis 4.

# *Analysis 3: Is the amount of stability within the matrix greater than expected at random?*

We also investigated whether there are more stable subsets within the observed community matrix than expected at random, using the Random positions and Random pairs models described above. One thousand seven-species random matrices were constructed under each model. All possible subsets within the observed matrix and within each random matrix were tested for stability.

The observed community matrix contained a greater number of stable subsets of every size than any of the 1000 Random-positions random matrices (Table 4). The Random pairs null model, with the competitive hierarchy retained, showed considerably greater numbers of stable subsets, though again on average fewer of each size than in the observed matrix. This confirms that the Botany lawn community matrix is closer to stability than expected at random, and that much of this stability can be attributed to the presence of a competitive hierarchy.

#### Analysis 4: Diagonal dominance and niche separation

One of the most important characteristics of community matrices influencing stability is the relationship between the diagonal and off-diagonal elements (Auerbach 1984). In competition communities, a tendency for the diagonal elements to be greater in magnitude than the off-diagonal elements enhances stability (Barnett and Storey 1970). In an extreme case, if for all rows the sum of the magnitudes of all off-diagonal elements is less than the magnitude of the diagonal element in that row, stability is guaranteed. Ecologically, this represents weaker interspecific interactions than intraspecific interactions, and is usually attributed to niche differentiation.

Manipulations of the Botany lawn community matrix showed its stability to be sensitive to small changes in its diagonal elements. For example, a uniform increase of only 2% in the diagonal values resulted in a reversal of the prediction from unstable to stable (2% is well within experimental error, though experimental error would not be uniform in direction). This confirms that the matrix is very close to the stability/instability boundary.

Two important features of the Botany lawn community matrix were revealed in the above analyses. First, the Botany lawn community is predicted to be close to the boundary of stability/instability. This was reflected both in the comparison of  $R(\lambda)_{max}$  for the observed matrix with the distribution of  $R(\lambda)_{max}$  derived under the various null models, and also in the sensitivity of the stability prediction to small perturbations of the matrix diagonal elements. Just how a real community close to the stability/instability boundary would be expected to behave is uncertain. Possible scenarios include a trend for the community to recover, but not fully, for some species to be able to recover but not others, and sensitivity of the community response to small changes in the nature of the perturbations, e.g. degree, timing or type.

Second, the tendency of the Botany lawn species to compete asymmetrically and form transitive competitive hierarchies was found to enhance the probability of stability in community matrices. This was observed as an increase in the probability of observing a stable community in the null models where both asymmetry and hierarchy were retained, and also in the analyses of the stability of subsets within the matrix.

#### Mechanisms of species coexistence

The proximity of the community matrix to the stability/ instability boundary, and the observation that many of the species within the lawn are able to coexist with one another (Roxburgh and Wilson 2000), raises the question of which mechanisms are enhancing coexistence.

#### Apparent mutualism

In multispecies mixtures, indirect effects (Levine 1976, Vandermeer 1990) can cause an interaction that is negative on a pairwise basis to become positive, preventing competitive exclusion and hence allowing longterm coexistence (Lawlor 1979). Tilman (1988) has called this type of indirect effect 'apparent mutualism', because in the context of the multispecies community direct competitors can behave as mutualists. Stone and Roberts (1991) provided an analytical method for identifying apparent mutualism. Their results showed that 20-40% of interactions which are competitive in pairwise isolation became mutualistic when they were embedded within multispecies competitive communities.

Apparent mutualism seems not uncommon in nature. Connell (1983) reviewed field manipulation experiments, detecting apparent mutualism by an decrease/increase in the abundance of one species in response to an experimental decrease/increase in another. He found two cases of apparent mutualism involving higher plants (viz. Allen and Forman 1976, Fowler 1981).

Table 4. The number of stable two-, three-, four-, five- and six-species mixtures within the estimated community matrix, and the average number of stable subsets for each from 1000 matrices constructed from each of the 'Random positions' and 'Random pairs' algorithms.

Subset size	6	5	4	3	2
Total possible	7	21	35	35	21
Observed no. stable subsets	1	10	18	31	20
Random positions					
Average no. subsets stable	0.0	0.1	1.2	6.6	10.0
Proportion random $\geq$ observed	0.00	0.00	0.00	0.00	0.00
Random pairs					
Average no. subsets stable	0.4	4.5	15.8	28.4	-
Proportion random≥observed	0.28	0.07	0.32	0.16	_

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Although we were unable to directly test for the presence of apparent mutualism in the Botany lawn, this is just the type of community where apparent mutualism might be expected to be found; there is strong competition between the species (Table 1), and all the species are well mixed, providing the opportunity for simultaneous multispecies interactions (Roxburgh and Wilson 2000).

#### Niche differentiation

It is unlikely that apparent mutualism is the only mechanism responsible for maintaining diversity in the Botany lawn. Eleven other possible mechanisms are known (Wilson 1990). Niche differentiation is almost certainly a contributory mechanism. We have demonstrated differences in vertical stratification in this lawn (Roxburgh et al. 1993), differences in guild membership (Wilson and Roxburgh 1994, Wilson and Watkins 1994), and there are obvious differences in growth form between species. For example, *Hydrocotyle heteromeria* is stoloniferous and forms a complex clonal network which weaves and scrambles amongst other 'non-mobile' species such as *Holcus lanatus*.

However, only niche differences which are independent of environment variability can be incorporated into the community matrix framework, due to the assumption of equilibrium. Despite this, niche differentiation can also arise in nature due to differential species responses to variable environmental conditions, either in space or time, giving rise to spatial and temporal niches. These fluctuation-dependent coexistence mechanisms are incompatible with the traditional community matrix approach, and hence require alternative methods of analysis to elucidate (Chesson 1994). Indeed, the exclusion of these potentially important mechanisms is a major limitation of the community matrix approach, and is discussed in greater detail in the 'Conclusions' section of the companion paper (Roxburgh and Wilson 2000). Although we chose the Botany lawn as a community which we thought would come close to satisfying the assumptions required by community matrix theory, we cannot guarantee that fluctuation-dependent mechanisms do not contribute to the maintenance of diversity in this community. For example, Hydrocotyle heteromeria has the ability under stress to replace above-ground parts using reserves in the rhizome (Sykes and Wilson 1990). This potential to buffer population growth against unfavourable environmental conditions is a key ingredient of many fluctuation-dependent mechanisms of coexistence, e.g. the storage effect (Chesson 1994), and thus suggests the possibility that this mechanism may also contribute to the coexistence of species in the Botany lawn.

#### Opportunity for coevolution

Apart from *Hydrocotyle heteromeria*, which is a native of New Zealand, the remaining six species are all native

to Europe and the British Isles (Clapham et al. 1987). More specifically, all of these species are common components of temperate grasslands, and where their ranges overlap they commonly coexist (Perring and Walters 1962, Grime et al 1988). Also, in Muller's (1990) study of approximately 800 lawns from 12 German cities, all six species were common components of the lawn flora. This suggests the possibility that these species have had the opportunity to coevolve traits to enhance coexistence, e.g. through the evolution of niche differentiation.

#### Limitations of the stability analysis

As indicated in the Introduction, the community matrix and the associated stability analyses are based on a number of simplistic assumptions. Although we chose to apply the theory on a community which we thought would approximate these assumptions, a number of problems were encountered in applying the theory to a natural community. Two problems which directly relate to the estimation of the matrix elements are discussed below. In the companion paper (Roxburgh and Wilson 2000), we discuss the relationship between community matrix theory and the dynamics of the Botany lawn, and more generally draw conclusions on the utility of community matrix theory for investigating stability in ecological communities.

# Difficulty in quantifying the interactions among all species in the community

One difficulty in applying the community matrix to real communities is the work required to measure the matrix elements, for this requires quantifying the interactions among all possible pairs of species in the community. For the Botany lawn there were 21 species recorded in the community; however, the maximum number we could use in the experiments was only seven, and even this required a large experimental effort. This is an important problem, because there is no guarantee that a subset of species chosen from a stable (or unstable) community should exhibit the same dynamic behaviour as the parent community (Table 4). The relatively strong competitive effect exhibited by the numerically rare Ranunculus repens suggests that all species have the potential to play an important role in community dynamics, not only those that are the most abundant in the community.

# *Difficulty in relating experimental results to community matrix theory*

Community matrix theory assumes a stable equilibrium point, with the matrix elements describing the dynamics around this equilibrium. We used competition experiments to estimate these elements; however, the assumption that such experiments can be used to infer the dynamics about an equilibrium point is far from certain (Wilson and Roxburgh 1992). This is because the matrix elements represent instantaneous pairwise effects measured when all other species in the community are held at their equilibrium values (Eq. 4), whereas the competition experiments quantify the direct pairwise effects, averaged over the duration of the experiment. In the case of the Botany lawn the situation is complicated further, because monitoring the actual community showed some within- and between-year variation in the dynamics of some of the species, therefore violating the strict definition of equilibrium specified by the theory (Roxburgh and Wilson 2000). The Botany lawn community matrix should therefore be regarded as the best estimate available, and these caveats should be borne in mind when assessing the stability predictions based on this matrix.

#### Experimental evidence of stability

In this paper we used an experimental approach, applying community matrix theory to an actual community, to make predictions of its stability. The resulting prediction of marginal instability, keeping the above caveats in mind, suggests a possible conflict with the actual behaviour of the community, as the Botany lawn has already persisted for 30 years. However, there are no records of the floristic composition of the lawn over this period. The only valid method of testing the prediction of marginal instability is by experimental perturbation of the community, and subsequent monitoring of its recovery. In the companion paper (Roxburgh and Wilson 2000) we report such an experiment.

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