Analysis of interspecific interactions in a coastal plant community—a perturbation approach

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Most studies of plant communities attempt to correlate species distributions with environmental variables. Such studies provide some insight into the contribution of density-independent variables to plant community structure, but contribute little to our understanding of niche relationships and levels of competitive interactions among coexisting species. In contrast, experimental perturbation studies where species are added or removed, have the advantage of testing specific biotic interactions among community components in natural conditions. Such approaches, for example, have proved valuable in elucidating the role of competition and predation in structuring sessile marine invertebrate communities. Despite an empirical approach championed by Clements, few terrestrial plant ecologists have conducted analogous perturbation–response studies. We have performed perturbation experiments on a set of closely adjacent coastal plant communities. Our observations indicate that species interactions are important in structuring these plant communities, and that these interactions may be specific or diffuse, reciprocal or non-reciprocal and may vary in different environments. We suggest a general approach to quantifying species interactions, derived from perturbation experiments, as a framework for generalizations and comparisons of biotic interactions in natural communities.

A series of adjacent coastal plant communities was examined along a gradient across Core Banks, a barrier island on the coast of North Carolina. The vegetation was surveyed by measuring optical point cover in 448 0.25 m² quadrats located along two main transects across the island and several smaller transects chosen to include the total range of communities encountered in the area. A single environmental scalar was developed from two measured environmental variables (distance from beach berm crest and depth to water table), using direct gradient ordination. From relative cover values, we obtained running average curves for each species along the scalar (Fig. 1). Detailed analyses of these ordinations will be presented elsewhere. Several workers have attempted to make interpretations regarding niche relationships among coincident species from such descriptive data, but these purely observational data beg the question of whether species both coexist and compete, or coexist because they do not compete. Experimental perturbations were carried out at five sites approximately 50 m apart along one of the main transects in the primary dune, rear dune, swale-grassland, high salt marsh, and low salt marsh. Dominant and subdominant species were removed singly or in groups within 1 m² plots by weeding, combined with selective herbicides. At each site there were two or four selective removal treatments (see Fig. 2 and Table 1), complete vegetation removal, plus a control. Grasses and sedges were spot- or broadcast-treated with Dalapon (2,2-dichloroproplionic acid) and diquatdyes with (2,4-dichlorophenoxyacetic acid (2,4-D). Treatments were repeated as necessary to ensure that vegetative regrowth did not occur during the first 3 months of the study (June–August). At each site, treatments were assigned randomly to cells in each of three replicate blocks. Four samples were taken per cell for a total of 12 replicates per treatment per site. Species responses were measured by optical point cover (0–81 counts per replicate) and, for grasses, by change in the number of tillers per year. The results of both methods were very similar, and only values based on optical point cover are presented (Fig. 2 and Table 1).

Removal effects were tested by analysis of variance (after square root transformation) in which treatments were contrasted with controls in paired comparisons. Using block × treatment mean square as the error mean square, significant removal treatment effects were found in 8 of 48 comparisons. The residual error of the treatments was ≤0.05 (1.2) [Table 2 and Table 1] whereas <3 would have been expected by chance at this level. We use this result to show that significant species interactions can potentially be resolved by such perturbation–removal experiments.

It is possible that the within-block replication differs from that between blocks; in this case it would be invalid to combine error variation. A subjective assessment of the experimental area indicated that the two levels of variation were similar for most of the cells. In addition, the mean square errors associated with the within-cell replicates were approximately equivalent to the block × treatment mean square errors for 40 of 48 comparisons. We therefore pooled the error variation for each comparison and have given the appropriate standard errors in Table 1.

We now introduce a general approach to analysing these biotic interactions: the response of species i to the removal of species j can be quantified in terms of a removal response coefficient defined as Ci,j = Ni,j/Ni, where Ni,j is the change in importance of species i following the removal of a coincident species j, and Ni, is the importance value of species i coexisting with species j before the imposed perturbation. Here importance values are based on per cent cover, but abundance, biomass, reproductive output and so on, might be used. Ni, is equivalent to the relative area of the central, darker circle in

Fig. 1 Direct gradient ordination for 16 herbaceous species occurring along the Core Banks, North Carolina transects. The environmental scalar is based on a weighted distance from the beach and the inverse of depth to the water table. Species curves were plotted from running averages. Abbreviations for species are as follows: Un, Uniola paniculata; Eu, Euphorbia polygalifolia; Sp, Spartina patens; Co, Conyza canadensis; Oe, Oenothera humifusa; Hy, Hydrocotyle lanata; Tr, Triodia spartea; So, Solidago sempervirens; Er, Erigonus pilosus; Mu, Muhlenbergia capillaris; Sb, Sbataea stricta; An, Andropogon scoparius; Fh, Phalaris spatica; Di, Ditrichis spicata; Ll, Lennum carolinianum; Sa, Spartina alterniflora.
each diagram of Fig. 2; \( N_i \) is equivalent to the relative area of the \( j \)th inner, tangential circle associated with each \( N_j \).

In most cases, coexisting species increased in importance after the removals. However, in one case, \textit{Eragrostis} showed a large decrease in importance (negative \( C_i \) value) following the removal of \textit{Spartina patens} from the swale. This effect has been confirmed recently in controlled competition experiments (data not shown). These observations are not necessarily consistent with any predictions that could be made from purely descriptive data (Fig. 1). For example, significant and apparently strong competitive interactions occur between \textit{Fimbristyliis} (i) and \textit{S. patens} (j) (\( C_{ij} = 0.498, C_{ji} = 0.693 \); see Fig. 2a and Table 1), species which have almost complete distributational overlap in the high marsh (compare with Fig. 1). However, little interaction is indicated between \textit{S. patens} and \textit{Uniola} (\( C_{ij} = -0.028, C_{ji} = -0.078 \); see Fig. 2a and Table 1) which have a similar distribution in the dune (Fig. 1). Again, from Fig. 1, the pattern of distributational overlap in the swale between \textit{Muhlenbergia} and \textit{S. patens}, \textit{Hydrocotyle}, \textit{Solidago}, \textit{Andropogon}, \textit{Paspalum} and \textit{Eragrostis}, varies continuously from inverse to broadly overlapping, yet significant interactions are revealed between \textit{Muhlenbergia} and at least two of the six associated species (\( C_{ij} = 0.055, 0.085, 0.130, 0.085, 0.065 \) and 0.100, respectively; see Fig. 2c and Table 1). Species interactions are abundant, but the way in which they structure these plant communities and lead to the zonation patterns observed in Fig. 1 is complex.

The interactions found were both specific and diffuse. We can quantify these based on the equitability of responses among \( j \) species to the removal of a particular species \( i \). A high equitability would indicate diffuse interactions whereas a low equitability would indicate species-specific effects. Using the standard Shannon information measure\(^{33}\), equitability \( E_i = H_i / H_{\text{max}} \), where

\[
H_i = - \sum_{i=1}^{s} \left( N_{ij} / \sum_{i=1}^{s} N_{ij} \right) \ln \left( N_{ij} / \sum_{i=1}^{s} N_{ij} \right),
\]

\( s = \) number of \( j \) species coexisting with \( i \), and \( H_{\text{max}} \) is equal to \( H_i \) calculated assuming that all \( N_{ij} \) values are equal. In the high

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<th>Retained (j)</th>
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SE, standard error of responses are based on combined error variation: within block mean square and block x treatment mean square. \( C_{ij} \) values were determined from back-transformed \( N_i \) and \( N_j \) values.

\* Mean cover values (after square root (\( x + 0.1 \)) transformation) for control and removal treatment.
marsh, removal of _S. patens_ produced a large and significant response from _Fimbristylis_ alone among six competitors (E = 0.225, for 4 of 6 competitors as listed in Table 1, Fig. 2d; absolute N values were used). This contrasts with the swale where there were no equal interactions among the six subdominant species after removal of _Muhlenbergia_ (E = 0.978; Fig. 2c).

Non-reciprocal responses seem common across these sites. We can define reciprocity of species _j_ with _i_ as _R_{ij} = C_{ij}/C_{ji}_, where _|C_{ij}| = |C_{ji}|_. In four of the five sites the interactions between the dominant and subdominant species were largely non-reciprocal. In the rear dune and low marsh, _R_{ij} = -0.064_ and _-0.813_, respectively, for _Hydrocotyle_ with _S. patens_ and _Spartina alterniflora_ with _S. patens_ (Fig. 2). Negative values would result from non-reciprocal contraction of species _j_ in response to the removal of species _i_. In the swale the dominant _Muhlenbergia_ was consistently involved in non-reciprocal responses with the three subdominant components: _S. patens_, _Andropogon_ plus _Eragrostis_, and _Hydrocotyle_ plus _Solidago_ (R = -0.010, -0.171, and -0.354, respectively; Fig. 2c). In the primary dunes, _S. patens_ and _Uniola_ both showed little interaction but _R_{ij} = -0.359_ (Fig. 2a). Only in the high marsh were the responses relatively reciprocal between _S. patens_ and _Fimbristylis_, _R_{ij} = 0.719_ (Fig. 2d).

Site-specific effects were also prevalent. The nature, degree and reciprocity of significant species interaction between _Hydrocotyle_ and _S. patens_ changed depending on the habitat considered: _C_{ij} for the primary dune = 0.857; C_{ij} and C_{ji} for the rear dune were 0.344 and -5.409, respectively; and C_{ij} and C_{ji} for the swale (_Solidago_ included with _Hydrocotyle_ in _i_) were -0.003 and 3.787 (Fig. 2a–c). Similarly the interactions of _S. patens_ with _Fimbristylis_ changed for high compared with low marsh (_C_{ij} = 0.498 and 0.722; Fig. 2d, e). We cannot distinguish whether these site-specific effects are a direct effect of the environment on the species interaction, or the result of changes in background species composition, or both.

One major problem in assessing species interactions by perturbation—response studies is that the results may be time-specific and biased towards fugitive species. However, we do not believe this is applicable to the present study. The complete removal treatments allowed us to identify _Sabalia_, _Salicornia_, _Triglochin_ and _Setaria_ as fugitive species because they were either absent or persisted at low frequency in the community and expanded following complete removals; only one of these species was found in one of the partial removal treatments. These results show that while our observations were time specific, they were not necessarily biased towards fugitive species. Clearly one could quantify fugitivity of a species by observing the change in its _C_{ij} with time; however this was not done in the present study.

This experimental approach, with the associated parameters, could be extended to the level of the entire community if all species were reciprocally removed. We could then examine interference among coexisting species across the community by considering a _C_{ij} matrix_, where the elements are removal response coefficients indicating covariation in abundance of species _i_ and _j_. Sets of covarying species can then be identified, and may be considered to constitute guilds. Moreover, the parameters relating to diffuseness and reciprocity of the interactions can be extended, by simple weighting, to the entire community, and can then be used for comparisons between different communities, or among different classes of species (based on, for example, abundance, life form or breeding system) within particular communities. By performing single species and multispecies removals, the existence of higher order community interactions can also be tested. We have deliberately avoided interpreting _C_{ij} in explicit biological terms: for example, _C_{ij} could be thought of as representing the degree of overlap in resource utilization of species _j_ on species _i_, but this is a presumption not warranted by either the nature of this study or any other perturbation experiment per se. Even if we excluded interaction effects due to predators or pathogens, deriving competition coefficients from such perturbation responses would require an _a priori_ assumption as to the appropriateness of the competition model used to make such calculations.

Clearly, the information about community structuring gained from such perturbation experiments is far greater and more accurate than any inferences that might be made from purely descriptive studies. Such experiments provide a definitive test
of interference among community components; the nature of this interference can then be tested either by constructing synthetic communities in controlled conditions, or by further field experimentation. Above all, when perturbation responses are quantified using the indices suggested here, they can be used in a comparative way, to generate and test hypotheses regarding the manner in which different communities are organized.

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Inhibition of experimental ascending urinary tract infection by an epithelial cell-surface receptor analogue


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It has been shown that the establishment of urinary tract infection by *Escherichia coli* is dependent on attachment of the bacteria to epithelial cells1–4. The attachment involves specific epithelial cell receptors, which have been characterized as glycolipids5–10. Reversible binding to cell-surface mannoses may also be important11–15. This suggests an approach to the treatment of infections—that of blocking bacterial attachment with cell membrane receptor analogues. Using E. coli mutants lacking one or other of the two binding specificities (glycolipid and mannose), we show here that glycolipid analogues can block *in vitro* adhesion and *in vivo* urinary tract infection.

Table 1 lists the properties of the *E. coli* strains used. *E. coli* HU 824 and HU 742 were selected after a two-step chemical mutagenesis of *E. coli* GR 12, isolated from a patient with acute pyelonephritis, as having either surface ligands attaching to epithelial cells through globoseries glycolipid receptors or mannose-reversible binding properties. The mutants HU 742 and HU 824 were obtained after N-methyl-N-nitro-N-nitrosoguanidine treatment of a lactose-negative mutant of GR 12. Further details on the construction and stability of the mutants will be reported elsewhere16. The mutants and the parent were identical by the following genotypic and phenotypic characteristics available for testing: electrophoretic mobility of 13 chromosomally determined enzymes17, three plasmid bands of the same size16, serotype17, resistance to the bactericidal effect of serum18, inability to haemolyse horse erythrocytes19 and api 20 E pattern. Clearly, these tests or other techniques are insufficient to demonstrate genetic identity between the mutants. The only discernible difference between these strains was, however, the receptor specificity of their adhesins. Initially, this

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<tr>
<td>Streptomycin</td>
<td>R</td>
<td>S</td>
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<tr>
<td>Naldixide acid</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Trimethoprim</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td>Sulphadiazine</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Tetracycline</td>
<td>S</td>
<td>S</td>
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<tr>
<td>Cephalothin</td>
<td>S</td>
<td>S</td>
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<tr>
<td>Mecillinan</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Ampicillin</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Nitrofurantoin</td>
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<td>S</td>
</tr>
<tr>
<td></td>
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<tr>
<td>Bactericidal effect of human serum</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Haemolysin production</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adhesion to uropathelial cells (bacteria per cell)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Human</td>
<td>65</td>
<td>0</td>
</tr>
<tr>
<td>Mouse</td>
<td>51</td>
<td>12</td>
</tr>
<tr>
<td>Receptor sugar inhibiting adhesion</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Globotranin</td>
<td>90 µg ml⁻¹</td>
<td>NI</td>
</tr>
<tr>
<td>α-Mn</td>
<td>NI</td>
<td>920 µg ml⁻¹</td>
</tr>
<tr>
<td>Agglutination of guinea pig erythrocytes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uncoated in PBS</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>in α-Mn</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Coated with globotranin-αMn</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>in PBS</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>in α-Mn</td>
<td>+</td>
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</tr>
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*E. coli* HU 824 and HU 742, mutants of a wild-type pyelonephritogen *E. coli* strain, were identical for the genotypic and phenotypic traits listed, but differed in specificity of their adhesins. R, resistant; S, sensitive; Kt, nontypable for Kanigens17. To permit separate detection out of a mixture, mutants resistant to 1 mg ml⁻¹ of streptomycin (HU 824 StrR) or to 50 µg ml⁻¹ of naldixide acid (HU 742 NatR) were selected by the gradient plate technique (without mutagenesis). The resistant mutants grew equally well on TSA with or without antibiotic after passage on antibiotic-free medium, retained the adhesive and haemagglutinating properties and showed no difference in *in vivo* infectivity compared with the respective parent. Adhesion to uropathelial cells from the urinary sediment of a healthy female donor (blood group Pp) and the bladder of BALB/c mice was assessed as described elsewhere1–2. Adhesion = mean no. of bacteria attached to 40 epithelial cells. For adhesion inhibition, bacteria were preincubated with decreasing concentrations of globotranin or α-Mn, epithelial cells were added and adhesion testing was performed5,7. The concentration required for 50% inhibition of the adherence of 10⁵ bacteria is shown. NI, no inhibition. Induction of binding of *E. coli* HU 824 StrR17 was studied by agglutination of guinea pig erythrocytes coated with globotranin-αMn18. Agglutination after but not before coating, and in the presence of α-Mn, was credited to the receptor. The oligosaccharide globotranin, released from globotranin by oxonolysis, and purified by Polsh partitioning and alkaline fragmentation, was analysed by gas-liquid chromatography and NMR (ref. 23). The NMR spectroscopy in D₂O spectrum showed signals from three anomic protons with chemical shifts, as expected for globotranin: β-hexosesamine, β-hexose and α-hexose. The fourth anomic signal from the reducing glucose residue was split into two, corresponding to the β and α form in the proportions 1:2.
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