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Experimental tests of trophic dynamics: towards a more penetrating approach

Abstract The complex interactions between primary producers, herbivores, carnivores, and detritivores have resulted in the burgeoning field of trophic dynamics. One important contribution is the Fretwell and Oksanen theory (FO theory). The FO theory proposes that the productivity of the environment determines the length of the trophic chain, which, they suggest, is directly related to whether the system is being controlled by top-down forces (odd numbered length of trophic chain) or bottom-up forces (even numbered length of trophic chain). Recent evidence from experiments by L.H. Fraser and J.P. Grime claims to support the FO theory but the methodology has been criticised by D.C. Moon, P. Stiling and M.V. Cattell for hidden treatments and pseudoreplication. We reject these criticisms and recommend an approach to the study of trophic dynamics involving the aggregation of organisms into functional groups, direct quantitative measurements of trophic processes using field manipulations, inferences based upon the use of field probes and synthesis of ecosystems in closed microcosms.

Key words Ecosystem · Functional groups · Methodology · Microcosm · Reductionist

Introduction

Moon et al. (1999) make a number of assertions in their critique of Fraser and Grime (1997, 1998), two major

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ones being that we ignored hidden treatments in our analysis, and that we are guilty of pseudoreplication. Their arguments are unconvincing, or based on a simple misunderstanding of our experimental procedure. We have raised what we believe to be an important current issue in this reply by asking the question "What are the conditions necessary for a tolerant and fruitful interaction between plant and animal ecologists in the study of trophic dynamics?" We conclude that a range of new methods are required to achieve a shift from descriptive studies to measurements of ecosystem processes. We suspect that the reductionist orthodoxy exemplified by Moon et al. (1999) explains in part the slow progress in testing the Fretwell and Oksanen (FO) hypothesis (Fretwell 1977, 1987; Oksanen et al. 1981; Oksanen 1990).

Field experiment

The first paper Moon et al. (1999) criticised was our examination of trophic dynamics along a natural productivity gradient in a North Derbyshire dale (Fraser and Grime 1997). In this experiment, we selected six plant community types which varied in productivity: two at high, two at moderate, and two at low productivity. Of the 20 plots from each community type 10 received above- and below-ground systemic insecticides and molluscicides throughout one growing season. The other 10 untreated plots were control plots. At the end of the growing season we harvested all above-ground biomass from each plot and compared, among other things, the change in total above-ground biomass mediated by pesticides. The only significant response we found was greater above-ground biomass at moderate productivity where pesticides had been applied. This result indicates that herbivory was strongest at moderate productivity, which supports the FO hypothesis.

There are two aspects of this experiment with which Moon et al. (1999) take issue: (1) hidden treatments; and (2) the use of bioassays. We will respond to each separately.

Hidden treatments

Moon et al. (1999) suggest that since diversity is highest at moderate productivity we have introduced a "hidden treatment" (*sensu* Huston 1997) which possibly confounds the result. However, Huston's discussion centred around highly manipulated, synthesized communities which were explicitly investigating the relationship between diversity, productivity and ecosystem properties. Since the experimental communities were artificially constructed, Huston was arguing that the investigators had neglected an opportunity for controlled manipulations of both species number and functional type. In our experiment which was conducted on naturally occurring plant communities there was no such opportunity to tease apart variation in species number and functional type. We are not denying that there is a relationship between productivity, plant functional types and diversity; far from it. This relationship is well established in plant ecology and has been termed the "hump-backed model" (Grime 1973, 1979). The hump-backed model proposes that species richness reaches a maximum at intermediate levels of biomass, which is indeed what our results for Tideswelldale show. It is therefore inevitable that field investigations along natural productivity gradients will encounter confounded variation in biomass, plant community architecture, species traits, species richness and many other organismal or environmental factors.

It is a well established principle (Grime 1965) that in studies of natural patterns (as distinct from experimental designs) correlated variation between ecological factors is an ever-present phenomenon and sets a limit to the explanatory power of individual pieces of fieldwork. However, the existence of such complications must not deter us from field studies which provide vital contacts with reality. Hence, we regarded the test of the FO hypothesis in our manipulative study in Tideswelldale as supportive rather than definitive and we considered it essential to document carefully any obvious confounded variation in features such as species-richness and to conduct other kinds of investigations (e.g. the microcosm experiments of Fraser and Grime 1998) that control for species diversity. We fully support the idea that it is necessary to examine the roles (if any) of plant species richness and plant community architecture in explaining the correlation between intermediate productivity and the maximum in herbivory. However, these have become valid research objectives only in the light of the results obtained in the Tideswelldale field experiment.

The use of probes

Historically, the study of trophic dynamics has been conducted by animal ecologists (Lindeman 1942; Hairston et al. 1960). This animal-centred approach has also resulted in criticism (Murdoch 1966), and has even spawned alternative methods involving theories of plant defence (e.g. Coley et al. 1985). We have approached the study of trophic dynamics from a plant perspective. We acknowledge that there are limitations when all the organisms are not known. Unfortunately, time, expertise, and resources were simply not available to collect and classify all the animals and fungi in each of the six communities. Obviously our support for the FO model could be significantly strengthened, or weakened, depending on the numbers of herbivores and carnivores found in each community. However, even pit-fall traps, vacuum sampling, and sweep nets would provide sketchy proof of herbivore and carnivore activity. In particular, many below-ground animals would not be caught. Also, even though the main herbivores were invertebrates, the main carnivores may have been small mammals, birds or parasites. Finally, animals are mobile and the community patches were relatively small so that movement between the patches was highly likely. Capture of an animal in one community would not prove that it is feeding in that community.

In order to estimate the effect of herbivores on the vegetation at each of our field sites we rejected inference based on animal census data in favour of direct measurement of the change in plant biomass following herbivore removal over a complete growing season. It is important to emphasize that these were by far the most important data we presented in support of the FO model. In addition, bioassays (probes) were used to obtain a "snapshot" of herbivore and carnivore activity; data consistent with the FO model were obtained. However, it would be foolish to place great reliance on assays involving single food items presented on a single occasion. In our discussion of these results we freely acknowledge that it would be unreasonable to expect lettuce and maggot assays to (quote) "unlock the complex workings of an ecosystem". In the discussion section of Moon et al. (1999) this careful qualification of a minor (but supportive) component of the work has been presented as illustrative of a general uncertainty on our part with respect to the whole investigation; this is an unbalanced, unfair, unscientific comment.

Microcosm experiment

The second paper commented upon by Moon et al. (1999) was an investigation involving factorial combinations of soil fertility, vegetation, an aphid species and a ladybird species in ventilated but enclosed microcosms. The experiment showed that selective feeding by the aphid modified the vegetation and that predation by the ladybird reduced aphid numbers and reduced their impact on the vegetation.

Moon et al. (1999) again suggest that our experiment has a hidden treatment and they also assert that our experimental design involved pseudoreplication.

Hidden treatment

When ecosystems are allowed to assemble in closed outdoor microcosms it is inevitable that carbon dioxide released from plants and soil micro-organisms will accumulate to levels higher than would be expected in open conditions. This is unlikely to exert a major impact on ecosystem development but we considered it important to demonstrate that variation in soil fertility and plant biomass in our experiment could not so modify the extent of CO_2 accumulation that this would constitute a hidden treatment (*sensu* Huston 1997). In order to deal rigorously with this problem we presented data on CO_2 levels from earlier experiments in which vegetation had been allowed to develop for a much longer period and at three levels of mineral nutrient supply, two of which correspond to those used in our grass:aphid:ladybird experiment. The results showed that our experimental treatments differed on average by 20 ppm, which corresponds to a difference of 2.9%. Set against a background concentration of approximately 700 ppm (twice ambient – the common level for testing enhanced CO_2 effects) we suggest that this difference was most unlikely to exert significant biological effects. Perhaps more to the point, nothing was "hidden"; *we* reported this difference.

Pseudoreplication

We think our methodology was adequately described. However, Moon et al. (1999) correctly point out an error which occurred in the analysis of our data presented in Tables 1 and 2 (Fraser and Grime 1998). In the original presentation of the data, biomass measurements from each pair of containers within a microcosm were pooled and analysed as part of the same replicate (Fraser 1996). Unfortunately, during the re-analysis of the data in preparation for submission to *Oecologia*, the data were inadvertently not pooled, and therefore the results presented in Tables 1 and 2 of Fraser and Grime (1998) are incorrect. Table 3, as well as the confidence

Table 1 Results of three-way ANOVA where the independent variables are soil fertility (*FERT*), plant species (*SP*), and the trophic treatment (*TROPHIC*), and the dependent variable is above-ground biomass. The table presents the sum of squares (*SS*), degrees of freedom (*df*), mean squares (*MS*), *F*-ratio, and *P*-values (*P*)

Source of variation	SS	df	MS	F-ratio	P
FERT	3073.056	1	3073.056	8.525	< 0.001
SP	3368.968	2	1684.484	634.288	< 0.001
TROPHIC	45.282	2	22.641	8.525	< 0.001
FERT × SP	1674.965	2	837.483	315.352	< 0.001
FERT × TROPHIC	31.805		15.902	5.988	0.004
SP × TROPHIC	119.564	4	29.891	11.255	< 0.001
FERT × SP × TROPHIC	91.052	4	22.763	8.571	< 0.001
ERROR	239.014	90	2.656		

Table 2 Results of two-way ANOVA examining the effects of the soil fertility treatment (*FERT*) and the trophic interaction treatment (*TROPHIC*) on the total above-ground biomass. This table presents the sum of squares (*SS*), degrees of freedom (*df*), mean squares (*MS*), *F*-ratios, and *P*-values (*P*)

Source of variation	SS	df	MS	F-ratio	P
FERT	9590.220	1	9590.220	767.294	< 0.001
TROPHIC	210.031	2	105.015	8.402	0.001
FERT × TROPHIC	157.726	2	78.863	6.310	0.005
ERROR	374.963	30	12.499		

limits and Tukey's test results presented in Fraser and Grime (1998), are correctly based on pooled data for each microcosm. We thank Moon et al. (1999) for directing this to our attention, thus allowing us to correct our error. We include here the corrected Tables 1, 2 based on pooled data for each microcosm. The results do not change the conclusions of Fraser and Grime (1998).

Conclusion

Criticism and debate is an integral part of science but it must be clearly thought out in order to be effective. Having read, digested, and discussed the critique by Moon et al. (1999) of our two papers (Fraser and Grime 1997, 1998) we continue to maintain that our papers lend strong support for the Fretwell-Oksanen model and we accept with enthusiasm this opportunity to reiterate our original conclusions.

The experience of responding to Moon et al. (1999) has alerted us to differences in research philosophy in the field of trophic dynamics. These differences appear to relate to disparities in outlook between some plant and some animal ecologists. We noted the concern of Moon et al. (1999) to compile complete inventories of the animals present in each plant community but we did not find a convincing explanation of how such data could be translated into a quantitative assessment of trophic interactions in ecosystems of contrasted productivity. The construction of detailed food webs is an interesting activity in its own right but we suspect that it does not provide the most direct route to a comprehensive test of FO theory. As an alternative capable of rapid application in a wide range of ecosystems we recommend an approach involving aggregation of organisms into functional groups, direct quantitative measurements of trophic processes using field manipulations, inferences based upon the use of field probes (*sensu* Fraser and Grime 1997) and synthesis of ecosystems in closed microcosms.

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