

Does the Fretwell–Oksanen model apply to invertebrates?

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Despite the myriads of herbivores in terrestrial ecosystems, the world is green (Hairston et al. 1960). Nevertheless, all these animals consume plant material and they should therefore have some influence on plant individuals, populations and communities. Hence, in order to understand community and ecosystem processes, we need a quantitative understanding of the impact of herbivores on plant communities and of its variability across ecosystems.

Many ecologists will agree, that invertebrates have a lower impact on plant communities than vertebrates (Crawley 1989). However, exclusion experiments revealed that invertebrates influence biomass, species richness, competition regimes and nutrient cycling in plant communities (Bach 1994, Brown 1994, Brown and Gange 1989, Carson and Root 1999, Fraser and Grime 1997, Gibson et al. 1990). Furthermore, the results of these experiments showed considerable variability of the herbivore effect across plant communities (Hendrix et al. 1988, Fraser and Grime 1997). One explanation for this variability is the so-called Fretwell–Oksanen model. Fretwell (1977, 1987), Oksanen (1990) and Oksanen et al. (1981) suggested that the relative importance of top-down and bottom-up forces within communities changes with productivity. A low primary productivity should not be sufficient to sustain appreciable populations of herbivores (bottom-up control of herbivores), whereas at high levels of productivity predators control herbivores (top-down control of herbivores). Hence, on the community level herbivore impact should show a hump at intermediate levels of productivity. Oksanen et al. (1981) and Oksanen (1990) emphasised that their model applies only to vertebrates. Invertebrates should have limited possibilities to respond on primary productivity, due to their low mobility, narrow dietary niche breadth and low costs of dormancy. Furthermore, invertebrate carni-

vores exploit also detritus-feeding prey and need little energy to run their physiological machinery throughout the year. Nevertheless, the Fretwell–Oksanen model has been applied to invertebrate grazing systems. The results of some recent studies provided some support for a hump-shaped pattern along nutrient gradients (Fraser 1998, Fraser and Grime 1997). Therefore, the objective of our study was to approach the following question: Do the available experimental results suggest a general hump-shaped relationship between productivity and the impact of invertebrate phytophages on plant communities?

The available data

We reviewed papers which report experimental data on the influence of phytophagous insects or molluscs on terrestrial plant communities. We conducted a search in the ISI Web of Science for articles published between January 1974 and July 2001. We searched titles, abstracts and keywords for a combination of the words (insect? or mollusc? or invertebrate?) and (herbivor? or phytophag? or defoliat?) and (plant communit?, “vegetation” or “top-down”) with “?” as a wildcard. Furthermore, we included all studies cited in the retrieved references. Most of these studies do not report primary productivity. We were forced to use standing crop as a surrogate of productivity and we included only studies where we were able to get data on standing crop measured by plant biomass (dry mass) of the herbivore-free treatment. At least for functionally and structurally similar plant communities a close relationship between primary productivity and above-ground biomass exist (Begon et al. 1996). We are aware of the high variability of tissue turnover rates in different perennial herb species, which may make standing crop a rather crude

measure of productivity. However, above-ground biomass differed by two orders of magnitude across studies, and subtle differences in the biomass-productivity relationship between plant communities should be of minor importance in the context of our study. For two studies, crude estimates of biomass were provided by the authors upon request.

If treatment means and standard deviations (or related parameters) were reported, herbivore impact was assessed as the effect size d (Gurevitch and Hedges 1993). F -values were transformed in effect sizes following Rosenthal (1991). Positive values of d indicate that herbivores decreased the biomass or plant cover of a plant community. For some long-term experiments it would have been possible to calculate an effect size for every year. Since most published studies report short-term experiments, we analysed only the results of the first experimental year in all cases.

To evaluate the overall effect of invertebrate herbivores, a grand mean across studies, its standard deviation and 95% confidence limits were calculated following Gurevitch and Hedges (1993). To test the Fretwell–Oksanen model, effect sizes were plotted vs above-ground plant biomass (log-scale). By fitting a second-order polynomial function, we tested whether the distribution of effects sizes shows a hump at intermediate levels of productivity. For each effect size the variance was estimated and effect sizes were inversely weighted by the variance (Hedges and Olkin 1985). Finally, we used selected quantiles (85%, 90%, 95%) to fit a second-order polynomial function to the upper boundary of the scatter (Cade et al. 1999; BLOSSOM software: Cade and Richards 1996).

Meta-analysis

We were able to extract 22 data points from nine published experiments. (Table 1). Note that not all data points are really independent and thus our analysis overestimates the degrees of freedom. These studies report four different types of experimental treatments: the exclusion of above-ground insects, exclusion of below-ground insects, exclusion of molluscs and exclusion of all invertebrates using selective insecticides or molluscicides. About 36% of the reports originated from Fraser (1998) and Fraser and Grime (1997), which excluded molluscs and insects. The exclusion of above-ground insects provided 32% of the data points, the exclusion of below-ground insects and molluscs comprised 23% and 9% of the data points. Across studies, the plant biomass of the plant communities varied from 1.8 to 1026 gram dry mass/m² in herbivore free treatments. Most studies were performed at sites of rather low primary productivity, only few deal with highly productive plant communities (Table 1). Furthermore,

most of the experiments were short-term experiments and were carried out in early successional communities.

We found a considerable variation of effect sizes, which ranged from slightly negative values to a nearly two-fold increase of above-ground biomass owing to herbivore exclusion (Brown and Gange 1989). In general, the exclusion of invertebrate phytophages caused positive responses of plant biomass or related measures (positive effect sizes more frequent than negative effects; sign test, $P = 0.02$). Across all effect sizes listed in Table 1, we found a grand mean of 0.57 ± 0.09 (standard deviation). The 95% confidence limits (0.38; 0.79) do not include zero. Hence across all experiments the data show clearly that invertebrate phytophages reduce biomass in plant communities. The experimental exclusion of only above-ground or below ground herbivores did not lead to smaller effect sizes (e.g. above-ground insects: 0.60, below-ground insects: 0.64). However, sample sizes are too small to allow for a meaningful statistical comparison of the experimental treatments.

Plotting the effect sizes of invertebrate phytophages versus plant biomass we found a rather scattered pattern (Fig. 1). Accordingly, the least square second-order polynomial model was not significant ($P > 0.3$). Furthermore, no relationship could be found for the different treatments with sufficient data (exclusion of above-ground insects only, exclusion of all insects and molluscs). However, the scatter suggested that its upper bound may support the Fretwell–Oksanen model. However, the second-order polynomial regression quantiles did not provide convincing support of a humped boundary. Two data points were identified as outliers (Dixon's test: $P < 0.05$, Sokal and Rohlf 1997): the study site with the lowest productivity value and the study with the highest effect size. Removing these two points from the analysis the 85th second-order polynomial regression quantile became marginally significant ($P = 0.09$).

If not primary productivity, which processes may contribute to the large scatter of the impact of invertebrate herbivores across ecosystems? First, productivity is correlated to other factors, which in turn interact with the impact of phytophages. For example species richness of plants may regulate herbivore effects (Moon et al. 1999, Mulder et al. 1999). Thus, because of complex and diffuse interactions within highly reticulated food webs, the relationship between productivity and diversity may confound the analysis of the relationship between productivity and impact of herbivores (Fraser and Grime 1999, Polis et al. 2000). This emphasises the complexity of biotic interactions that may mould patterns in natural communities (Oksanen and Oksanen 2000, Polis et al. 2000). Second, local patterns are the result of local and regional processes (Huston 1999). Thus only at localities where the regional setting and regional processes allow insects to build up considerable local populations, the Fretwell–Oksanen model

Table 1. Publications used in the meta-analysis and description of the study sites and the experimental treatments, above-ground biomass in the herbivore-free treatments, effect sizes (d), variances (v) and weights (w).

source	habitat	locality	excluded herbivores	above-ground plant dry mass [g/m ²]	d	v	w
Brown and Gange (1989)	old field	Berks/England	above-ground insects	approx. 250	3.876	0.58	1.74
Brown and Gange (1989)	old field	Berks/England	below-ground insects	approx. 250	1.613	0.27	3.77
Brown et al. (1988)	calcareous grassland	Berks/England	above-ground insects	approx. 150	1.940	0.25	4.08
Carson and Root (1999)	<i>Solidago altissima</i> dominated old field	Ithaca/USA	above-ground insects	296.5	-0.219	0.10	9.94
Fraser (1998)	<i>Urtica dioica</i> -stand	North Derbyshire/England	insects and molluscs	54.0	0.048	0.25	4.00
Fraser (1998)	grassland	North Derbyshire/England	insects and molluscs	81.5	1.354	0.31	3.25
Fraser and Grime (1997)	<i>Sedum acre</i> -stand	North Derbyshire/England	insects and molluscs	1.50	-0.227	0.20	4.97
Fraser and Grime (1997)	<i>Festuca ovina</i> dominated stand	North Derbyshire/England	insects and molluscs	11.3	-0.305	0.20	4.94
Fraser and Grime (1997)	grassland	North Derbyshire/England	insects and molluscs	48.6	1.546	0.26	3.85
Fraser and Grime (1997)	grassland	North Derbyshire/England	insects and molluscs	69.5	2.247	0.33	3.06
Fraser and Grime (1997)	<i>Urtica dioica</i> -stand	North Derbyshire/England	insects and molluscs	127.5	0.176	0.20	4.98
Fraser and Grime (1997)	<i>Petasites hybridus</i> -stand	North Derbyshire/England	insects and molluscs	20.7	0.094	0.20	4.99
Shure (1971)	old field	New Jersey/USA	below-ground insects	279.1	0.478	1.03	0.97
Hulme (1996)	meadow	Berks/England	below-ground insects	203.8	0.380	0.41	2.46
Hulme (1996)	meadow	Berks/England	molluscs	203.8	1.004	0.45	2.22
Hulme (1996)	grassland	Berks/England	below-ground insects	201.9	-0.008	0.40	2.50
Hulme (1996)	grassland	Berks/England	molluscs	201.9	0.101	0.40	2.50
Uriarte and Schmitz (1998)	old field	Connecticut/USA	above-ground insects	523	-0.362	0.20	4.92
Uriarte and Schmitz (1998)	old field	Connecticut/USA	above-ground insects	503	0.884	0.22	4.56
Uriarte and Schmitz (1998)	old field	Connecticut/USA	above-ground insects	525	1.189	0.24	4.25
Jung et al. (2000)	old field	Sachsen-Anhalt/Germany	above-ground insects	1026.0	0.505	0.23	4.35
Jung et al. (2000)	old field	Sachsen-Anhalt/Germany	below-ground insects	1026.0	0.581	0.13	7.83

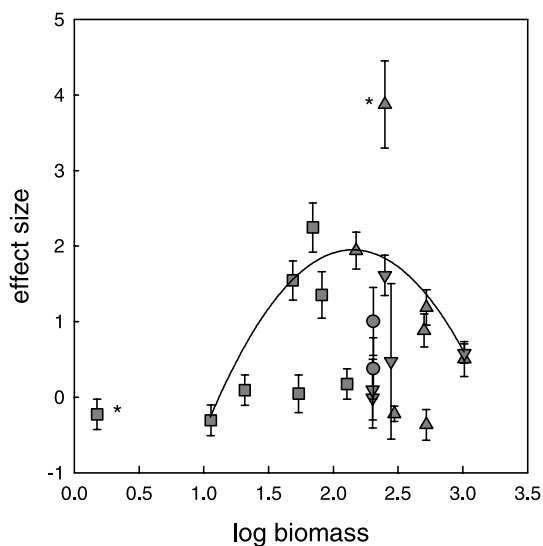


Fig. 1. Relationship between effect size of the exclusion of invertebrate herbivores on herbaceous or grassland plant communities and above-ground plant biomass (dry mass [g], see Table 1). Symbols refer to different exclusion treatments: exclusion of above-ground insects ▲, exclusion of below-ground insects ▼; exclusion of molluscs ●; exclusion of all insects and molluscs ■. Line represents the second-order polynomial function using 85th regression quantiles after removing two outliers (indicated by asterisks; Dixon's test: $P < 0.05$). Biomass values refer to the herbivore-free treatment and, therefore, do not include the herbivore effect.

may apply. Third, most of the studies in our meta-analysis were performed within successional communities. Such communities are not in equilibrium. Plants may be out of step with the environmental conditions and the invertebrates may not have adjusted to the plant community.

Conclusion

Our analysis provides clear evidence that phytophagous insects have some impact on plant communities. However, we found little support for the Fretwell–Oksanen model. Hence our analysis supports the arguments made by Oksanen et al. (1981, 1997), Oksanen (1988) and Oksanen and Oksanen (2000) that their model applies to vertebrate herbivores but not invertebrates. In addition to this theoretical and experimental evidence against the Fretwell–Oksanen model in invertebrate-plant systems (see also Wardle 2002 for soil food webs), it is further possible that covariations of other factors with site productivity confound the analysis of the relationship between invertebrate impact and productivity. Hence, there is still a need for well-designed exclusion experiments across a wide range of primary productivities. The need for further experimental work is highlighted by the fact, that nearly all statistical

calculations in our analysis suffered from low sample sizes.

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