

Field evidence and model predictions of butterfly-mediated apparent competition between gentian plants and red ants

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Abstract

In recent spatial models describing interactions among a myrmecophilous butterfly *Maculinea rebeli*, a gentian *Gentiana cruciata* and two competing species of *Myrmica* ant, we predicted that apparent competition should exist between gentians (the food of young *M. rebeli* caterpillars) and *Myrmica schencki*, which supports *M. rebeli* in its final instar. Here we extend and quantify model predictions about the nature of this phenomenon, and relate them to ecological theory. We predict that: (i) Within sites supporting the butterfly, fewer *M. schencki* colonies occur in sub-areas containing gentians than in identical habitat lacking this plant. (ii) Where *G. cruciata* and *M. schencki* do co-exist, the ant colonies will be less than half the size of those living >1.5 m from gentians; (iii) The turnover of *M. schencki* colonies will be much greater than that of other *Myrmica* species in nest sites situated within 1.5 m of a gentian. All three predictions were supported in the field on 3-6 sites in two mountain ranges, although the exact strength of the apparent competition differed from some model predictions. Field data were also consistent with predictions about apparent mutualisms between gentians and other ants. We suggest that apparent competition is likely to arise in any system in which a specialist enemy feeds sequentially on two or more species during its life-cycle, as occurs in many true parasite-host interactions. We also predict that more complex patterns involving other *Myrmica* species and *G. cruciata* occur in our system, with apparent competition existing between them in some sub-areas of a site being balanced by apparent mutualism between them in other sub-areas.

Keywords: Apparent competition, enemy-free space, community module, population dynamics, *Myrmica*, *Maculinea*, *Gentiana*.

Résumé

Dans de récents modèles spatiaux décrivant les interactions entre un papillon myrmécophile *Maculinea rebeli*, une gentiane *Gentiana cruciata* et deux espèces de fourmis *Myrmica* en compétition, nous avons prédit qu'une compétition apparente devait exister entre les gentianes (desquelles se nourrissent les jeunes chenilles de *M. rebeli*) et *Myrmica schencki* qui nourrit les larves de *M. rebeli* plus âgées. Dans cet article, nous étendons et quantifions les prédictions du modèle sur la nature de ce

phénomène et les liens à la théorie écologique. Nous prédisons que : (i) dans les sites où vit le papillon, on trouve moins de colonies de *M. schencki* dans les parties de ces sites contenant des gentianes que dans des habitats identiques sans gentianes ; (ii) là où *G. cruciata* et *M. schencki* co-existent, les colonies de fourmis seront inférieures de plus de la moitié à celles installées à plus de 1,5 m d'une gentiane ; (iii) la rotation des colonies de *M. schencki* sera bien plus importante que celle d'autres espèces de *Myrmica* dans les nids situés à moins de 1,5 m d'une gentiane. Ces trois prédictions se sont vérifiées sur le terrain sur 3 à 6 sites dans deux massifs montagneux, bien que l'importance exacte de la compétition apparente diffère de certaines prédictions du modèle. Les données de terrain sont également en cohérence avec les prédictions sur le mutualisme apparent entre les gentianes et les autres fourmis. Nous suggérons que la compétition apparente peut survenir dans tout système dans lequel un ennemi spécialiste se nourrit séquentiellement au détriment de deux espèces ou plus au cours de son cycle de vie, comme c'est le cas dans de nombreuses véritables interactions hôte-parasite. Nous prédisons également que des patrons plus complexes impliquant d'autres espèces de *Myrmica* et *G. cruciata* existent dans notre système, avec une compétition apparente entre ces espèces dans certaines parties de ces sites, et un mutualisme apparent dans d'autres.

INTRODUCTION

The Palaearctic butterfly *Maculinea rebeli* Hir. has a complex life-cycle that impacts on the populations of at least three other species (fig 1a). Its caterpillars feed first on the flowers of *Gentiana cruciata* L. before living as social parasites inside *Myrmica* ant nests, where they compete with ant larvae for food (ELMES *et al.*, 1991 a, b). *Myrmica schencki* Emery is the main host of *M. rebeli*, but other species of *Myrmica*, which compete with *M. schencki* for nest sites, also adopt many caterpillars (THOMAS *et al.*, 1989). Although *M. rebeli* seldom survives to adulthood in non-host *Myrmica* nests, its caterpillars can cause substantial reductions to the next generation of worker ants in them; even greater damage is done to infested *M. schencki* colonies. Indeed, six of the eight interactions in this food-web of two ants, a butterfly and a gentian (fig. 1a) are known to be strong (HOCHBERG *et al.*, 1992, 1994), making it a promising system with which to examine apparent competition (HOLT, 1977) and other patterns (CLARKE *et al.*, 1997) that result from the indirect or direct interactions between species in communities.

The term "apparent competition" was coined to describe situations in which two or more species that do not directly interact are, nonetheless, hindered from coexisting in the presence of a shared enemy species, which they support as prey and which differentially harms them both (HOLT, 1977, 1984; HOLT *et al.*, 1994; HOLT & LAWTON, 1993, 1994). In reviewing the consequences of possessing shared enemies, HOLT and LAWTON (1994) defined a wide range of situations in which apparent competition may exist. Several empirical studies support this theory (*e.g.* SCHMITT, 1987; SETTELE & WILSON, 1990; MENGELE, 1995; MÜLLER & GODFRAY, 1997), but because none makes explicit reference to population models, it has been difficult to assess how generally applicable their results may be (R. D. HOLT, pers. comm.).

In this paper we attempt to combine theory with empiricism by employing a partially validated model of the *M. rebeli* system (HOCHBERG *et al.*, 1994; ELMES *et al.*, 1996) to make specific predictions about apparent competition which are then assessed against field data. Due to the endangered status of *M. rebeli* (ANON, 1991), it was not possible to make manipulative experiments to test predictions. Instead, we used the model using parameters from one *M. rebeli* site in the Spanish Pyrenees to make qualitative and quantitative predictions about the co-existence of gentian and ant

populations in space and time, and then measured whether the predicted patterns existed on other *M. rebeli* sites, mainly in the French Alps.

THEORETICAL FRAMEWORK: THE SYSTEM STUDIED AND NEW PREDICTIONS ABOUT APPARENT COMPETITION

Biology

The biology of the system is described extensively elsewhere (ELMES & THOMAS, 1987 *a, b*; ELMES *et al.*, 1991 *a, b*, 1996; THOMAS, 1994; THOMAS & ELMES, 1993; THOMAS *et al.*, 1989, 1991, 1993, with additional data in HOCHBERG *et al.*, 1992, 1994). The following points are relevant to this paper, and satisfy the ten criteria listed by HOLT & LAWTON (1994) that enable our example to be integrated with theory and other studies.

The 'enemy' species in our system is the butterfly *Maculinea rebeli*; the 'victims' its early larval foodplant *Gentiana cruciata* and two populations of *Myrmica* ant which support *M. rebeli* in its final instar. Typical sites supporting this community are 0.25-1ha sub-alpine meadows, with clear-cut boundaries defined by the distribution of *G. cruciata*. Adult butterflies oviposit freely throughout the site on flowering gentians, but seldom emigrate. Their young caterpillars develop rapidly on gentian flowers, fall to the ground and await discovery by foraging *Myrmica* workers, which mistake them for ant larvae and carry them into their nests. Caterpillars cannot disperse more than a few cm from the gentian, and die if they are not within the short (c. 1.5 m) foraging range of a *Myrmica* colony. Once in the ant nest, each caterpillar feeds on the resources of its colony for 10 months, increasing >50-fold in weight before pupating. Although adopted by any *Myrmica* species that happens to forage under gentians, *M. rebeli* survives to adulthood almost exclusively in the colonies of *Myrmica schencki*, the 'host' ant. The caterpillar causes substantial harm to *M. schencki* colonies and considerable, but less, damage to the other *Myrmica* colonies that adopt it. These non-host species – consisting of *M. rubra*, *M. scabrinodis* and *M. sabuleti* on most sites – are lumped together as a super-population ('Other *Myrmica*') in our models.

Myrmica, *G. cruciata*, and *M. rebeli* interact and function at different temporal and spatial scales, and at two trophic levels within a site. The butterfly is univoltine. *G. cruciata* is perennial, with a clumped distribution, site densities ranging from 38 to 2672 plants ha⁻¹, and a niche that extends from cool moist ground inhabited by *Myrmica rubra* and *M. scabrinodis*, through intermediate zones where *M. rubra*, *M. scabrinodis*, *M. sabuleti* and *M. schencki* compete, to sparse arid turf where *M. schencki* dominates or competes with other ant genera, such as *Lasius*, *Formica* and *Taponoma*. Each ant colony forages up to c. 1.5 m from the nest entrance and functions as a discrete population. Thus a 1 ha meadow, supporting solitary populations of the butterfly and the gentian, effectively contains a metapopulation of up to 900 *Myrmica* colonies (CLARKE *et al.*, 1997). Individual ant colonies are highly dynamic. Small colonies frequently go extinct and vacant nest sites are soon colonised by offshoots from large neighbouring colonies. On average, unparasitised *Myrmica* colonies survive for 10 years, but those adopting *M. rebeli* (*i.e.* those within 1.5 m of a gentian) disband more often, especially those of *M. schencki* which are seriously damaged by the caterpillar. This makes the density of gentians on a site an important parameter

(ELMES *et al.*, 1996), modulating the damage the butterfly inflicts on ants. The two *Myrmica* 'species' considered – *M. schencki* and 'Other *Myrmica*' – compete for nest sites wherever their niches overlap; the balance between them varies locally, depending on (i) the precise quality of the habitat, which affects their respective intrinsic growth rates $r_{M. schencki}$ and $r_{\text{Other Myrmica}}$, and (ii) whether they are within 1.5 m of flowering gentian(s), in which case each ants' growth rate for a given habitat quality is differentially reduced by the impact of the butterfly. However, no direct interaction has been recorded between *G. cruciata* and *Myrmica*; for example, the shade cast by *M. cruciata* is negligible compared to that of other plants in the sward.

In theory, the interactions between these four species (fig. 1a) exemplify one of the simpler food-web modules that may generate apparent competition (HOLT & LAWTON, 1994). It is also one of the least diffuse. Although embedded in a wider species-rich community (MUNGUIRA, 1987), the *Myrmica-Gentiana-Maculinea* module is largely insulated from the influence of other species because: (i) *G. cruciata* is a robust perennial, unpalatable to most herbivores and phytophagous insects; (ii) *Myrmica* ants are keystone species that dominate their environment and compete mainly between themselves; (iii) *M. rebeli* spends 95% of its life-cycle isolated inside the gentian flowers or underground with *Myrmica*, and no major density dependent mortalities are known to affect it outside of the module. Thus the species of this module are likely to exhibit clearer patterns of interaction in the field than other interacting species that are less segregated from their wider community.

Models of the *Maculinea-Myrmica-Gentiana* community module

Two basic models have been constructed to describe population interactions in the above system (HOCHBERG *et al.*, 1992, 1994). Certain predictions have been empirically confirmed on 12 other sites, indicating that the foundations of the models are sound (ELMES *et al.*, 1996). Features relevant to this study are described from the HCET (1994) model which, through being spatially explicit, is the better suited for studies of apparent competition.

The HCET model is highly mechanistic, incorporating 19 parameters measured either on a Pyrenean grassland (S1) or in the laboratory. The model site consists of a grid of 30×30 cells equal to a total area of 1 ha (figs 1 b-d), with each cell corresponding to the foraging range of a typical *Myrmica* colony and containing at most one nest. Micro-variation in habitat is represented by a linear gradient along the x axis of the grid, ranging from cool-moist to hot-dry cells in 30 steps. Each species of *Myrmica* has a different growth rate and nest capacity according to its position across this gradient. Non-host *Myrmica* persist in cells $x = 1-22$ peaking at $x = 9$, whereas *M. schencki* inhabits cells $x = 9-30$, with maximum productivity at $x = 22$ (fig. 1b).

The model is seeded with ants and run for 30 'years' allowing the ants to reach a dynamic balance (fig. 1 b). *M. rebeli* is then introduced in low numbers to interact sequentially with the gentians and ants; no further recruitment of any species occurs from outside the habitat patch. It is important to note that caterpillars cannot disperse and only enter ant colonies that co-exist with a gentian plant within a cell. As individual ant colonies die or are driven extinct by caterpillars, the vacated cells are occupied by stepping-stone colonisation from any adjacent ant colony that is above a threshold size; we assumed that the first ant colony to arrive in a vacant cell cannot be displaced that year by neighbouring nests, and that adoption of *M. rebeli* occurs after the completion of the annual ant colony dynamics (HOCHBERG *et al.*, 1994). After

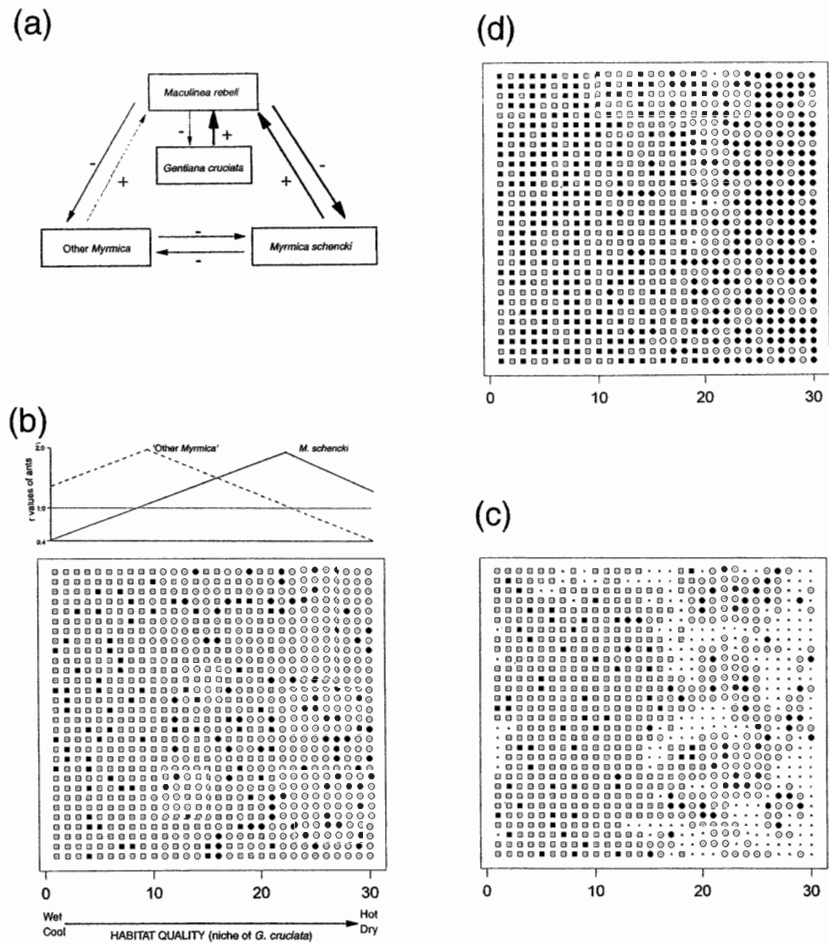


FIG. 1. – Food-web and representation in spatial models of the *Myrmica-Gentiana-Maculinea* community module. (1a) Interactions between the four species involved; sign and direction of arrow indicate beneficial (+) or harmful (-) impact of one species on another species' population; boldness of arrow indicates approximate strength of the relationship. (1b-d) The 30 × 30 grid used for spatial models of the system. (b) The occupancy of cells in the HCET model (site S1), containing 2672 *G. cruciata* plants ha⁻¹, before the butterfly invades. Also indicated is the gradient of habitat quality along the x axis and the effect of this on the intrinsic growth rate (r_{max}) for each ant species. (c) The same site 50 years after the butterfly has invaded. (d) A more typical site than S1, containing fewer (900 ha⁻¹) *G. cruciata* plants.

Key

- *M. schencki* + *G. cruciata*
- *M. schencki*, no *G. cruciata*
- 'Other Myrmica' + *G. cruciata*
- 'Other Myrmica', no *G. cruciata*
- x *G. cruciata* but no *Myrmica*
- Blank cell indicates sub-area not occupied by any species

a few butterfly generations, the abundance and local distribution of the two *Myrmica* populations are radically changed, with *M. schencki* largely driven out of cells containing gentians, especially where this ant's intrinsic growth rate is low. The snapshot shown in figure 1c is, however, atypical of most sites, because gentian densities were exceptionally high at S1. Most sites resemble figure 1d (ELMES *et al.*, 1996), where the comparative lack of gentians provides local refuges for *M. schencki*, enabling it to persist better in sub-optimal parts of its niche.

Predictions of apparent competition

Earlier models of the *Maculinea* module were not concerned with apparent competition between *G. cruciata* and *M. schencki*, although the possibility was highlighted. We therefore reran the HCET model for more explicit predictions, also modifying it to use both average (900 plants ha⁻¹) and below average (400 plants ha⁻¹) gentian densities and clumping parameters recorded elsewhere (ELMES *et al.*, 1996). Predictions were taken following runs for 30 'years' without the butterfly, then a further 50 years after *M. rebeli* had invaded, corresponding to the intermediate, trans-generational time-scale of HOLT & LAWTON (1994) for balanced populations.

We found that the strength and nature of apparent competition varied within and between model sites depending on local habitat quality (which affects the intrinsic rate of increase for each ant colony) and gentian density (which affects the number of ant refuges). Its strength in any local patch can be described by HOLT & LAWTON's (1994) 'core criterion' for victim (ant) persistence: $r > aP$, where r is the victim's intrinsic rate of increase, a = enemy (butterfly) attack rate and P = enemy abundance. In our example, interspecific competition between ants is an additional factor. In the absence of the butterfly, *Myrmica schencki* can persist in cells $x = 10$ -30 of the habitat gradient on the original model site (fig. 1b). After *M. rebeli* has invaded, $aP > r$ in cells 10-14 and 30 of the gradient (where the value of $r_{M. schencki}$ is low), usually resulting in this ant's elimination from these sub-optimal habitat patches if they contain gentians. In habitat-type 15-29, *M. schencki* is merely diminished near gentians (fig. 1c).

The situation with 'Other *Myrmica*' is complex and more interesting. The final outcome of the butterfly's impact depends not only on the value of $r_{\text{Other Myrmica}}$ for each habitat patch but also – in intermediate types of habitat – on the extent to which the direct damage by the butterfly is compensated by its greater impact on competing colonies of *M. schencki* (fig. 1a). On sites with either density of gentians (figs 1c, d), the net effect of the butterfly is beneficial to 'Other *Myrmica*' in most types of intermediate habitat, with both models predicting weak 'apparent mutualism' (*sensu* HOLT & LAWTON, 1994) between 'Other *Myrmica*' and *G. cruciata* in cells $x = 10$ -16 of the gradient (cf. figs 1b and 1c). But in both wetter and slightly drier types of habitat where, respectively, *Myrmica schencki* never competes (cells $x = 1$ -9) or where $r_{\text{Other Myrmica}}$ is very low ($x = 17$ -22), the net effect of the butterfly is harmful to 'Other *Myrmica*', and apparent competition is predicted between this ant and gentian plants.

Using this framework, we obtained model predictions about three different attributes of the apparent competition or mutualism between *G. cruciata* and ants to test in the field. Because of the segregation of our module from other fauna and flora, we also predicted that these three patterns should be clearly identifiable on any *M. rebeli* site. However, since the strength of *Gentiana-Maculinea-Myrmica* interactions varies considerably between sites according to gentian density, clumping, site

size, shape, average micro-habitat quality, and the local distribution of microhabitat patches (ELMES *et al.*, 1996; CLARKE *et al.*, 1997), we would not expect the precise figures predicted – for example for average ant colony size near and away from gentians – to be the same on every site.

Prediction 1: Presence or absence of Myrmica near gentians

For any given category of micro-habitat quality, a colony of *M. schencki* will occur less often in a patch if *G. cruciata* also grows there. Specifically, for site S1 (high gentian densities) we predict that 51 % of all cells that lack *G. cruciata* will contain *M. schencki*, whereas only 28 % of otherwise identical cells that contain *G. cruciata* will support this ant, a ratio of 1: 0.5. For sites with average gentian densities (900 ha⁻¹), the figures are 50 % and 39 % respectively, a ratio of 1: 0.8; sites with 400 gentians ha⁻¹ are similar (Table I).

We predict smaller differences in the overall status of ‘Other *Myrmica*’ on sites with average gentian densities because the negative-negative and negative-positive chains of interactions are more balanced (fig. 1a). Specifically, we predict that 50 % of cells with no gentians will contain ‘Other *Myrmica*’ whereas 61 % of cells with gentians will contain the ant on typical sites, a ratio of 1: 1.2. We predict a similar situation on sites with abundant gentians (e.g. S1), with 47 % and 50 % of cells without and with gentians, respectively, also containing ‘Other *Myrmica*’, a ratio of 1: 1.2 (Table I).

Although not included in the model, we also suggest that ants belonging to different genera from *Myrmica* should show weak apparent mutualisms with gentians, because they compete with *Myrmica* to a limited extent yet the butterfly has no impact on them (e.g. ELMES *et al.*, 1991a).

Prediction 2: Size of Myrmica schencki colonies

On sites occupied by *M. rebeli*, those *M. schencki* colonies that do coexist with gentians will be smaller than those > 1.5 m away. For the site S1, the model predicts an average of 192 workers per colony near gentians compared with 1 088 away from gentians, a ratio of 1:5.7. The predicted impact is less on sites with lower gentian densities and hence more enemy-free space. At average gentian densities the model predicts an average of 318 workers per ant colony near gentians, rising to 435 workers per colony at low gentian densities (Table II).

Prediction 3: Turnover of M. schencki colonies

The model predicts that extinction and colonisation rates of *M. schencki* in patches where gentians grow will be high, exceeding the turnover rates of other *Myrmica* species by nearly fourfold on our S1 site.

FIELD TESTS OF MODEL PREDICTIONS

Sites and methods

We examined predictions 1 and 2 in the French Hautes Alpes in 1996, in three isolated meadows near Gap and St Etienne. Site descriptions are given in ELMES *et al.* (1996) under F1 (0.6 ha, 1 050 gen-

tians ha⁻¹), F3 (0.5 ha, 930 gentians ha⁻¹) and F5 (0.5 ha, 740 gentians ha⁻¹), although shape and micro-habitat quality and spatial heterogeneity, were not recorded. We also re-examined unpublished field data collected (with other objectives) on various *M. rebeli* sites in 1983-95 to explore predictions 2 and 3. All sites studied supported sufficiently high densities of *M. rebeli* for the butterfly to have a substantial (predicted) impact on *Myrmica* populations; all sites were also known to have supported *M. rebeli* for at least 8 years so, as in the model predictions, we studied patterns resulting from interacting populations in rough equilibrium, rather than in the immediate aftermath of enemy invasion.

Prediction 1: Presence or absence of ants near gentians

A total of 270 ant baits were placed on the ground on sites F1, F3 and F5, using techniques described by ELMES *et al.* (1996). The baits were laid in 135 pairs. In each pair, one bait was placed within 15 cm of a *G. cruciata* plant and the other in habitat of the same quality (including vegetational cover) 3-4 m away from the same plant and at least as far from any other gentians. All ants attracted to these baits were identified using a 20x hand lens in the field.

Prediction 2: Size of M. schencki colonies

A rough measure of colony size near and 3-4 m from gentians was obtained by counting the number of *M. schencki* workers attracted to the above pairs of baits, using the following size categories: 1, 2-3, 4-9, 10-19, and 20+ workers. In addition, we excavated and counted every worker in 55 *M. schencki* nests situated within 2.5 m of a flowering gentian and in another 17 nests that were >2.5 m away from a gentian on five *M. rebeli* sites in July 1983-96. On ELMES *et al.*'s (1996) list, the sites were F6 & F2 (1983, n=5; 1984, n=15; 1985, n=3; 1987, n=6; 1988, n=7), F1 (1996, n=10), S1 (1990, n=10; 1991, n=16) plus an unclassified site near the French-Italian border (1995, n=1).

Prediction 3: Turnover of Myrmica colonies

A crude measure of the turnover of *Myrmica* colonies near gentians was obtained in 1990-94 on site S1. For five consecutive years, baits were placed beneath the same 50 *G. cruciata* plants in early August, at the time of *M. rebeli* adoption. Each sample was >3m from the next, and the ants attracted to baits were identified to species (*i.e.* 'Other *Myrmica*' were broken down into *M. sabuleti*, *M. scabrinodis* and *M. rubra*). Although we could not detect when a colony disappeared if it was replaced by another of the same species, we could compare the frequency with which *M. schencki* was attracted to the same baits in consecutive years, and compare it with the frequency with which each of the other three *Myrmica* species came or went each year at each of the 50 fixed points.

RESULTS

Prediction 1: Presence or absence of ants near gentians

The results of placing pairs of baits in identical habitat within 15 cm and 3-4 m from 135 gentians are summarised in table I. The general pattern was as predicted: significantly fewer baits near gentians attracted *M. schencki*, the proportion attracting 'Other *Myrmica*' was similar in both situations, while ants from other genera were recorded more often under gentians, although this 'evidence' for apparent mutualism is not statistically significant ($P=0.14$).

Quantitatively, the observed number and ratio of *M. schencki* colonies foraging in the two scenarios is similar to (indeed stronger than) that predicted by the HCET

model for sites with high gentian densities ($2\ 672\ \text{ha}^{-1}$), but less so for sites with lower densities of gentians. In the case of 'Other *Myrmica*', the ratio of ants observed near and away from gentians was similar to that predicted (Table I, column no. 3), although in both situations the absolute number of baits attracting ants was lower than the model predicts.

TABLE I. – Observed and predicted proportions of 135 pairs of baits attracting ants on three *Maculinea rebeli* sites. One of each pair of baits was placed within 15 cm of a *Gentiana cruciata* plant; the other was in identical habitat 3–4 m away from the same plant. Model predictions for three gentian densities are given in italics.

Ant species	Site or Model	(1) Positive baits 3–4m <i>G. cruciata</i>	(2) Positive baits near <i>G. cruciata</i>	No. paired baits	(3) Ratio 2:1	Test	χ^2 , P
<i>M. schencki</i>	F3	25	9	39		1 ≠ 2	3.99, P<0.05
	F5	25	12	37		1 ≠ 2	2.67, ns
	F1	16	4	39		1 ≠ 2	3.96, P<0.05
	Σ obs.	66	25	135	0.4	1 ≠ 2	9.29, P=0.002
	<i>model (hi.)</i>	<i>69</i>	<i>38</i>	<i>135</i>	<i>0.5</i>	<i>o ≠ e</i>	<i>1.47, P=0.23</i>
	<i>model (av.)</i>	<i>67</i>	<i>53</i>	<i>135</i>	<i>0.8</i>	<i>o ≠ e</i>	<i>6.19, P=0.01</i>
	<i>model (low)</i>	<i>63</i>	<i>53</i>	<i>135</i>	<i>0.8</i>	<i>o ≠ e</i>	<i>7.20, P=0.007</i>
Other <i>Myrmica</i>	F3	9	4	39		1 ≠ 2	ns
	F5	12	21	57		1 ≠ 2	ns
	F1	9	6	39		1 ≠ 2	ns
	Σ obs	30	31	135	1.0	1 ≠ 2	ns
	<i>model (hi.)</i>	<i>63</i>	<i>78</i>	<i>135</i>	<i>1.2</i>	<i>o ≠ e</i>	<i>0.35, P=0.56</i>
	<i>model (av.)</i>	<i>67</i>	<i>82</i>	<i>135</i>	<i>1.2</i>	<i>o ≠ e</i>	<i>0.31, P=0.58</i>
	<i>model (low)</i>	<i>72</i>	<i>82</i>	<i>135</i>	<i>1.1</i>	<i>o ≠ e</i>	<i>0.10, P=0.75</i>
Other ant genera	F3	15	22	39		1 ≠ 2	ns
	F5	30	35	57		1 ≠ 2	ns
	F1	12	24	39		1 ≠ 2	ns
	Σ obs	57	81	135	1.4	1 ≠ 2	2.10, P=0.14

Prediction 2: Size of *M. schencki* colonies

For those baits that attracted *M. schencki* in the 'paired-bait' experiment, the number of workers per bait under gentians was consistently lower than that on the baits 3–4 m away (fig. 2), with an average of 3.7 workers and 7.5 workers respectively per bait in the two situations. Similarly, excavations of *M. schencki* colonies on various *M. rebeli* sites in 1984–96 showed that the average size of a colony near gentians was half (0.48) that of a colony > 2.5 m from *G. cruciata* (table II). This ratio is similar to that predicted by our model (0.4) for sites with low gentian densities, although the absolute size of *M. schencki* colonies away from gentians was consistently overestimated in all model predictions.

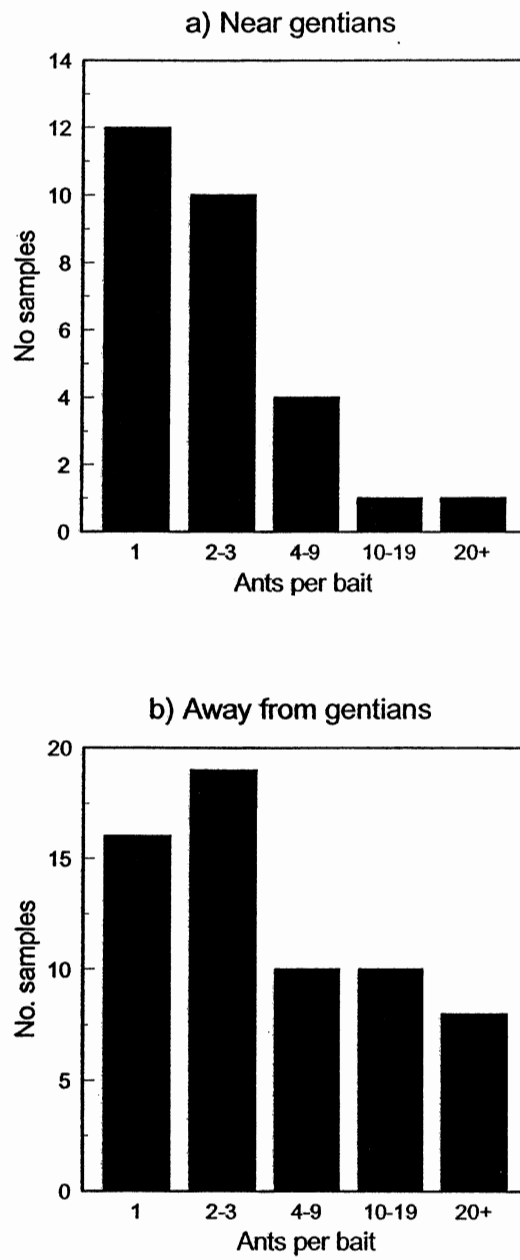


FIG. 2. – The number of *Myrmica schencki* workers attracted to paired baits placed (a) within 15 cm of *Gentiana cruciata* and (b) 3-4 m away from the same *G. cruciata* plants.

TABLE II. – The mean size (number of workers) of *Myrmica schencki* colonies excavated within 2.5 m of flowering *Gentiana cruciata* plants on four *Maculinea rebeli* sites in eight years in 1983-1996 compared with the mean size of 17 colonies that were >2.5 m from flowering gentians on the same sites (Normal script). Colony sizes predicted by HCET model are in italics.

	(1) Colonies >2.5 m from <i>G. cruciata</i>			(2) Colonies near <i>G. cruciata</i>			Ratio	
	Mean size	SE	N	Mean size	SE	N	1:2	P
Obs.	606	100	17	291	31	55	0.5	$P_{1<2} = 0.0038$
<i>Exp. (high)</i>	<i>1088</i>			<i>192</i>			0.2	
<i>Exp. (av.)</i>	<i>908</i>			<i>318</i>			0.3	
<i>Exp. (low)</i>	<i>1110</i>			<i>435</i>			0.4	

Prediction 3: Turnover of *Myrmica* colonies

Baiting under the same 50 gentians for five consecutive years at site S1 suggests that the turnover in *M. schencki* colonies is considerably higher than in other species of *Myrmica* (Table III). The observed number of annual changes in the presence or absence of *M. schencki* under individual plants was 1.8 times greater than that for the sum of the other individual *Myrmica* species present. Significant though this difference is ($P < 0.001$), it is less than the ratio predicted by our model, which suggested that species changes involving *M. schencki* should be 3.8 times greater than those involving any other individual *Myrmica*. However, the model also predicts much lower absolute rates of species turnover at fixed points near gentians than we recorded in the field.

TABLE III. – Turnover of colonies of different *Myrmica* species within 10 cm of *Gentiana cruciata* on a Spanish *Maculinea rebeli* site.

Ant species in year i	Changed species in years $i \rightarrow i+1$	No change in species in years $i \rightarrow i+1$	Colony turnover: <i>M. schencki</i> > Other <i>Myrmica</i> χ^2	P
<i>M. schencki</i>	30	7		
<i>M. sabuleti</i>	18	18	7.8	0.01
<i>M. rubra</i>	15	32	20.1	0.001
<i>M. scabrinodis</i>	13	4	(0.7)	ns
Σ non-host <i>Myrmica</i>	46	54	13.5	0.001

DISCUSSION

The field data support three aspects of apparent competition predicted for *M. schencki*, as well as general predictions made about 'Other *Myrmica*' and apparent mutualisms between *G. cruciata* and ants of other genera. We acknowledge that none of the three independent approaches taken constitutes a perfect test; some involved analysis of existing (unpublished) data for predicted patterns, while obvious experiments, such as removing all *M. rebeli* from certain gentians over several years, were not possible due to the rarity of this IUCN Red data book butterfly. However, the fact

that we found all the patterns of small-scale community structure predicted by our models on every site examined in two mountain ranges makes us confident that the predictions were, at least qualitatively, correct. These results complement empirical confirmation of other predictions from these models about relationships between the size and stability of butterfly and gentian populations (ELMES *et al.*, 1996). Together, the two sets of field results suggest that the basic models and their predictions are sound.

The match between field data and some quantitative model predictions was less close. We never expected an exact match because each study site differed in other unmeasured attributes that affect the strength of apparent competition, such as average micro-habitat quality (CLARKE *et al.*, 1997) and within-site variation in gentian densities. In general, we observed similar ratios of numbers near or away from gentians to those predicted, but the absolute values often differed, with the model usually predicting larger and less dynamic ant colonies than were actually found. We suspect that the first of these two discrepancies explains most other quantitative differences between model predictions and field data. Table II suggests that the original HCET model should have been calculated to have nearly twice as many *Myrmica* colonies on a site than we included, each containing an average of 600 rather than 1 100 workers per nest site and a correspondingly smaller foraging area. This would have little effect on certain model predictions, such as the carrying capacity of a site for the butterfly, but would affect the ant dynamics: an increased number of smaller *Myrmica* colonies would result in many more colonies falling below the threshold at which extinction becomes probable, leading to the greater turnover of colonies at individual nests sites that we found in the field (Table III). This would probably also result in even clearer patterns of apparent competition than were predicted, as we also found in the field. We recognised, when constructing the original models, that ant colony size and growth rates were the least reliably measured of the parameters included (HOCHBERG *et al.*, 1992, 1994). We conclude that their values should now be altered in the light of data published here.

The *M. rebeli* community module is unusual, but by no means unique, because it involves apparent competition resulting from strong indirect interactions between species from radically different taxa. Although our system contains several criteria (*see* "Theoretical Framework...") identified in theoretical biology as being likely to generate apparent competition between victim species (HOLT & LAWTON, 1994), other attributes differ fundamentally from the examples in previous reviews, which centred mainly on generalist predators. The shared enemy species in our food-web is an extreme specialist (the butterfly) that has evolved to 'prey' sequentially on two victims (the gentian and ant) during its life-cycle. This obligate sequential exploitation of two prey, whose life-cycles are more than an order of magnitude longer than that of their enemy, logically leads to apparent competition between the victims if (as in this case) the enemy has a serious impact on one or more of its victim's populations. In these respects our example resembles a true parasite-host interaction, where the parasite has an intermediate and definitive host, and a shorter life-cycle than either of its hosts. In model simulations we found no combination of (high) gentian densities and clumping that resulted in *Myrmica schencki* populations being entirely excluded from a *M. rebeli* site, because the butterfly is always driven extinct first by the reduction in its main resource; however, under certain habitat conditions it was theoretically possible for the ant populations to be reduced by about 90 % (CLARKE *et al.*, 1997). We

suspect that the same principle will apply to all systems in which apparent competition results from the obligate sequential feeding of one species on two or more resources.

The system we describe is also unusual in that it includes another (lesser) impact by the enemy on a minor alternative prey species ('Other *Myrmica*') that competes directly with the focal ant victim. This, in combination with within-site variation in r for both ants (caused by minor variation in local habitat quality), leads to complex chains-of-species interactions. One interesting prediction is that apparent competition should exist between gentians and 'Other *Myrmica*' in parts of a site where either *M. schencki* is absent or the value of $r_{\text{Other Myrmica}}$ is low, and apparent mutualism should exist between the same species in other sub-areas of the site where *M. schencki* is abundant. Although this prediction has yet to be confirmed in the field, it seems likely that different patterns of distribution may exist between populations in any system that contains species that interact both indirectly and directly, if the relative strengths of each population's impacts on the other vary according to a position along an environmental gradient.

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