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Parasite–grass–forb interactions and rock–paper–scissor dynamics: predicting the effects of the parasitic plant *Rhinanthus minor* on host plant communities

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Summary

1. Parasitic plants affect the growth, reproduction and metabolism of their hosts and may also influence the outcome of competitive interactions between host species and, consequently, the structure of entire host communities.

2. We investigate the effect of the root hemiparasitic plant *Rhinanthus minor* on plant community dynamics using a spatial theoretical model. The model is parameterized with data from pairwise interaction experiments under two nutrient levels between the hemiparasite and three grass species (*Cynosurus cristatus*, *Festuca rubra* and *Phleum bertolonii*) and three forb species (*Leucanthemum vulgare*, *Plantago lanceolata* and *Ranunculus acris*).

3. Relative interaction coefficients were intransitive, with the dynamics of the system conforming to a rock–paper–scissors game. Stable deterministic dynamics emerge from parameters obtained under low-nutrient conditions. Under high-nutrient conditions, the dynamics are unstable, but are stabilized in spatially explicit models. The outcomes are sensitive to initial spatial pattern and frequency.

4. *Synthesis*. This study supports the idea that hemiparasite populations may form 'shifting clouds' in natural populations and explains seemingly unpredictable shifts in host community structure following introduction of hemiparasites. Management of plant communities using hemiparasites needs to take these complex dynamics into account.

Key-words: competition, diversity, food web, niche, nutrients, root hemi-parasite, species coexistence

Introduction

Parasitic angiosperms are represented in the majority of ecosystems and provide an important model system for investigating the impacts of parasites on ecosystem functioning. Parasitic plants exploit host resources through haustoria that attach to the host plant (Musselman & Press 1995; Riopel & Timko 1995). Hosts suffer from suppressed biomass accumulation, reduced reproductive output (Seel & Press 1996; Cameron *et al.* 2005; Cameron, Coats & Seel 2006; Cameron & Seel 2007) and disrupted metabolic processes (Cameron *et al.* 2008). Parasitic plants may also influence the outcome of competitive interactions between host species (Gibson & Watkinson 1991; Matthies 1996; Cameron *et al.* 2005) and consequently, the structure of entire host communities (Callaway & Pennings 1998).

Rhinanthus minor is a root hemiparasitic plant widely distributed throughout natural and semi-natural grasslands in northern temperate regions of Europe and North America. As a hemiparasite, *R. minor* can undertake some independent photosynthesis but is still reliant on its hosts for a major proportion of its carbon and mineral nutrition. *Rhinanthus* has a wide host range (Gibson & Watkinson 1989) but its impact is not consistent across all host species (Ameloot, Verheyen & Hermy 2005; Cameron *et al.* 2005). Grasses are damaged to the greatest extent whilst forbs (non-leguminous perennial dicots) are left undamaged (Joshi, Matthies & Schmid 2000). This difference is due to the expression of resistance responses in forbs which is absent from the grasses (Cameron *et al.* 2005; Cameron, Coats & Seel 2006; Cameron & Seel 2007).

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Consequently, the parasite can shift the balance of a community in favour of forbs at the expense of grasses (Westbury 2004; Ameloot, Verheyen & Hermy 2005; Cameron *et al.* 2005; Westbury & Dunnett 2007).

Despite the recent breakthroughs in understanding the basis for parasite-induced host damage by *R. minor*, there appears to be extreme variability in the outcome of *R. minor* infestation on the structure and diversity of plant communities (Westbury 2004; Ameloot, Verheyen & Hermy 2005; Cameron *et al.* 2005). For example, host suppression by *R. minor* has been found in some studies to reduce community diversity (Gibson & Watkinson 1991), while other studies have suggested that the long-term presence of *R. minor* can promote diversity through the provision of 'regeneration niches' or available space for other species to colonize (Joshi, Matthies & Schmid 2000). It has also been suggested that short-lived hemiparasites such as *R. minor* may exist in a community as 'shifting clouds', depleting hosts in a given area then invading new territory only to re-invade previously occupied areas once the host community has recovered (Kelly 1989).

Identifying the mechanisms responsible for the variable outcomes of experiments and observations is difficult because the precise details of the interactions may differ in subtle ways. Thus host nutrient status (Cameron *et al.* 2005) and even the point of parasite attachment (Keith, Cameron & Seel 2004) have been shown to influence the net effect of *R. minor* on its host. Cameron, Coats & Seel (2006) showed robust resistance to *R. minor* by the forbs. As a result, the parasites were unable to extract the forbs' resources due to physiochemical barriers expressed by the host at the point of parasite attachment (Cameron & Seel 2007). In contrast, such defences were not expressed by the grasses (Cameron, Coats & Seel 2006) and the parasite had free access to its host's resources extracting and absorbing up 17% of host xylem solutes (Cameron & Seel 2007).

Mathematical modelling approaches have been rarely applied to investigate the dynamics of parasitic plants. An exception was the study of Smith (2000), who showed that hemiparasites could theoretically co-exist stably with their hosts even when they were competing for a single resource. Moreover, Smith (2000) showed that whereas only transitive interactions are possible in three-species mixtures with competition for a single resource, more complex interactions (including rock–paper–scissors type intransitive interactions) are possible if one of these species is a hemiparasite.

In this study, we investigate the potential effects of *R. minor* on host communities using a simple model of community dynamics parameterized with values derived from pairwise interaction experiments (Cameron 2004; Cameron *et al.* 2005; Cameron, Coats & Seel 2006). As conjectured by Smith (2000), these experiments revealed that many of the interactions involving hemiparasites are likely to be 'intransitive' (i.e. there is no ordered hierarchy for superior and inferior competitors). Previously, based on the results of pairwise competition experiments with non-parasitic species, intransitive competitive interactions have generally been thought to be rare in plants (Shipley 1994). Such intransitive competitive interactions can result in 'rock–paper–scissor' games, the dynamics of which have been extensively analysed in behavioural and animal ecology (May & Leonard 1975; Reichenbach, Mobilia & Frey 2007).

Using empirically derived measures, we show that complex, unpredictable dynamics can also emerge in hemiparasite–host communities, and that the outcomes are dependent upon the spatial structure of the community.

Materials and methods

EXPERIMENTAL STUDIES

These have been previously reported in Cameron (2004) and Cameron *et al.* (2005); Cameron, Coats & Seel (2006) and we therefore only briefly describe the methods. Twenty individual seedlings of 2-week-old host plant species (grasses: *Cynosurus cristatus, Festuca rubra* and *Phleum bertolonii;* forbs: *Leucanthemum vulgare*, *Plantago lanceolata* and *Ranunculus acris*) were grown for 4 weeks in 15 cm diameter pots. These species were selected as common constituents of natural and semi-natural grasslands that regularly co-occur with *R. minor*. Plants were grown in pots containing a 50:50 mixture of sand and John Innes compost. Half of the pots received 85 mg of nitrogen (N) per litre of substrate (low N), the remaining half received 250 mg of nitrogen (high N) per litre of substrate applied as potassium nitrate. *Rhinanthus minor* seed were surface-sterilized for 5 min in 3% sodium hypochlorite solution, washed in distilled water and preconditioned on moist filter paper at 4 °C until germination (*c.* 8 weeks). Four seedlings of *R. minor* at a time were transplanted into five of the pots containing the High N substrate and five pots containing the Low N substrate for each host species. Subsequently, the parasites were reduced to one per host when the first parasite showed morphological changes associated with attachment (as defined by Klaren & Janssen 1978). Attachment of the parasite to all hosts occurred within 5 days of the first attachment. The hosts together with the parasites were then grown for a further 14 weeks in a glasshouse (maximum temperature = 28 °C, minimum temperature = 16 °C, daily watering), then above-ground biomass of both hosts and parasites was harvested, dried at 80 °C for 48 h and the biomass recorded. Parasites were also grown in pots under the same conditions described above but in the absence of a host plant. The number of parasite flowers and parasite seed set was also recorded (see Cameron *et al.* 2005; Cameron, Coats & Seel 2006; Cameron & Seel 2007).

MODELS

We explored the potential consequences of parasite–grass–forb interactions using a simple difference equation modelling approach, based on data from the experiments described above. More complex models incorporating differences in life history, dispersal and density dependence among the components gave qualitatively similar results, but involved making more assumptions about parameter values (for which no precise data was available). Therefore, we present only the results of the simplest models.

NON-SPATIAL MODEL

We assumed interactions among community components occurred in a pairwise manner (as in the experiments) and that the frequency of these interactions was proportional to the representation of the components in the community. As we had no information on density dependence of these interactions, we assumed constant numbers and considered only changes in the frequency of the components. This is probably not unrealistic in dense grassland sward communities. The dynamics are described by difference equations of the following form, where P, G and F represent the frequencies of the parasite, grass and forb, respectively, at the subscripted time interval.

$$\begin{aligned} P'_{t+1} &= P_t(w_{PP}P_t + w_{PG}G_t + w_{PF}F_t) \\ G'_{t+1} &= G_t(w_{GP}P_t + w_{GG}G_t + w_{GF}F_t) \qquad \text{eqn 1} \\ F'_{t+1} &= F_t(w_{FP}P_t + w_{FG}G_t + w_{FF}F_t) \end{aligned}$$

Here, the superscript indicates that the frequencies are corrected by the total, and w_{ij} = the pairwise interaction coefficients of component i when grown with component j (where i, j = parasite, grass or forb). A stability analysis of this model is presented in Appendix S1 in Supporting Information, and the results are discussed below in the context of this study.

The interaction coefficients were calculated as the ratio of the dry-weight yield of the plant when grown with a second species, divided by its dry weight when growing on its own (see Table 1 for values). As the experiment was only a partial replacement series design that did not include each of the species grown at half density, it was not possible to formally distinguish conspecific from interspecific interaction effects (hence we did not calculate formal 'competition coefficients'). However, it is clear from both the magnitude and direction of the effects (and associated anatomical observations of the host–parasite interactions; Cameron, Coats & Seel 2006) that the large differences between grasses and forbs in response to challenge by *R. minor* were the result of differences in the nature of the parasitic relationship, and not because of highly different responses of grasses and forbs to conspecific competition (i.e. density effects). Values for each of the three species of grass and each of the three species of forb when grown with the parasite (and vice versa) were averaged by functional group. As there was no experimental data on the interaction between the grass and forb species, we made the assumption that the grasses would outperform the forbs (Del-Val & Crawley 2005). Furthermore, Gibson & Watkinson (1992) showed that the removal of *R. minor* resulted in the grass *Holcus lanatus* outcompeting surrounding forb species, a situation that is reversed in the presence of the parasite. We assumed values of $w_{GF} = 1.25$ for the grass and $w_{FG} = 0.8$ for the forb (Table 1) to be consistent with reciprocal effects and greater competitive ability of grasses versus forbs. Varying these values, with $w_{GF} > 1$ and $w_{FG} < 1$, did not affect the qualitative outcome, except at some extreme values. We explored the consequences of varying these values theoretically (see Appendix S1 and Results).

The use of dry weight is justified because in most plant populations individual dry weight correlates well with longevity and seed production, and hence lifetime fitness. In the present study, total seed production was also measured in *R. minor*. There was a strong correlation between dry weight and seed production in this species ($R^2 = 0.97$ for both High N and Low N; data not shown).

SPATIAL MODEL

We used a two-dimensional lattice consisting of a square grid of 40 × 40 cells, within each of which the dynamics are described by equation 1. We imposed stochastic variation by assuming a fixed population size (K) within each cell and assuming establishment was a binary variable; thus we sampled the numbers of parasites, forbs and forbs in each generation within a cell according to binomial expectations given the predicted frequency of each component from eqn 1.

Migration occurred from a given cell at a rate m into the orthogonally adjacent four cells on the lattice. Migration occurred by seed production and was assumed to be deterministic at the local level. However, to add an element of realism (and to avoid our results being determined by purely local dynamics), we incorporated a low level of long-distance migration by assuming a small fraction ($m = 0.01$, unless otherwise stated) of the total seeds produced in the lattice was distributed equally, but randomly, to each cell in the lattice according to Poisson expectations, prior to calculating the individual recursions in eqn 1. Boundaries of the lattice were absorbing (with individuals dispersed beyond the lattice 'falling off' at the edge).

Table 1. Dry weights (mg) of community components (left column) when grown pairwise with themselves or with other species of the community (top row), under high and low nitrogen. Numbers in bold italics show the average per individual yield in mixture and yield in pure stand standardized to 1 for intraspecific interactions (i.e. the interaction coefficients w_{Pi}, w_{Gi} and w_{Fi}, where i = P, G or F). Species of each component are from top to bottom as follows: parasite – *Rhinanthus minor*; grasses – *Phleum bertolonii, Cynosurus cristatus* and *Festuca rubra*; forbs – *Ranunculus acris*, *Leucanthemum vulgare*, *Plantago lanceolata*. Note: grasses were not grown with forbs, and the interaction coefficients represent default values used in the simulations (unless otherwise stated)

	High nitrogen			Low nitrogen		
	Parasite	Grasses	Forbs	Parasite	Grasses	Forbs
Parasite	100.0	375.0	74.2	38.4	211.7	50.6
		333.5	16.8		298.1	50.4
		209.0	7.4		115.8	9.5
w_{Pi}	***1***	***3.06***	***0.33***	***1***	***5.43***	***0.96***
Grasses	1276.5	1752.4	–	626.2	1035.9	–
	1099.2	1940.7	–	397.3	778.1	–
	624.0	789.9	–	170.4	450.2	–
w_{Gi}	***0.69***	***1***	***(1.25)***	***0.50***	***1***	***(1.25)***
Forbs	722.4	–	677.1	392.0	–	308.9
	1897.3	–	1933.4	1309.9	–	1341.2
	2231.3	–	2371.9	1360.9	–	1055.2
w_{Fi}	***1.00***	***(0.8)***	***1***	***1.18***	***(0.8)***	***1***

Results

NON-SPATIAL MODEL

The model using the interaction coefficients from the experiments under high N resulted in dynamics that were highly unstable (Fig. 1a), showing ever-increasing amplitudes in frequency and eventual dominance of one type over another. The outcomes (frequency and amplitude of the oscillations, and the 'winner' after 1000 generations) were sensitive to variation in the starting frequency of the components, but not in any clearly predictable fashion (data not shown). The ever-increasing amplitudes resulted in extreme frequencies of each type such that in any finite population it would rapidly lead to the initial extinction of one or another of the components and to the eventual collapse of the community to a single species.

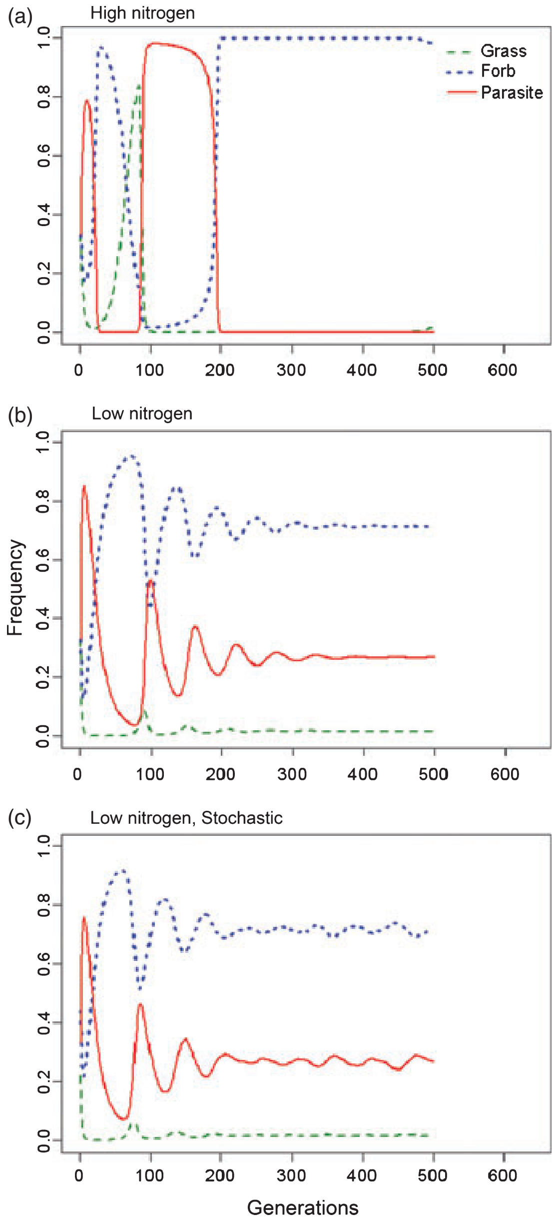

Fig. 1. Change in frequency of parasite, grass and forb components in a plant community without spatial structure. Interaction coefficients are as in Table 1 for (a) high nitrogen, (b) low nitrogen, (c) low nitrogen in a finite but large population.

However, when the model used parameters from the experiments under low N, a stable equilibrium was reached with a high frequency of forbs, a substantial frequency of parasites and a very low frequency of grasses (Fig. 1b). In finite populations, because of the low frequency of grasses and large fluctuations in population numbers, the grass component was often lost and the community became dominated by forbs.

We used the theoretical stability analysis and computer simulation to explore the generality of our results (see Appendix S1 in Supporting Information). In the competition experiments, grasses were not competed against forbs, so we assumed the values of $w_{GF} = 1.25$ and $w_{FG} = 0.8$. The stability analysis showed that the result of stable equilibrium under low N and unstable cycles under high N is robust under the assumption that grasses outcompete forbs in a relatively reciprocal manner (the constraints $w_{GF} > 1$, $w_{FG} < 1$; bottom right region of Fig. 2a, b). When the grass and forb show overyielding ($w_{GF} > 1$, $w_{FG} > 1$), it is possible to obtain stable equilibria under the results for the high N treatments (upper right region of Fig. 2b). For the low N treatment, there is only a very small region of unstable cycles, consistent with stable coexistence for $w_{GF} > 1$, $w_{FG} < 1$ over a broad range of values (right hand region of Fig. 2b).

To understand what caused the dramatic difference between the results for low and high N in the theoretical analysis, we fixed the parameters at the high N levels and then systematically changed one parameter at a time to the low N value to see if one parameter is responsible for the boundary shifts. It appeared that no single parameter changed the pattern dramatically (results not shown). However, if the values of w_{FP} and w_{PF} were both changed to those observed under low N (keeping other parameters at high N levels), the stable–cycles boundary is changed dramatically (the two other parameter combinations changed in this manner did not have this effect on the boundary). Therefore, the change in the parasite–forb interaction between high N and low N is largely responsible for the change in dynamics predicted for the two nutrient treatments.

This was confirmed when the forb–parasite parameters were varied pairwise (Fig 3a,b). It is clear that high or low N has little impact on the parameter portraits. However, the dynamics are very sensitive to the actual values of w_{PF} and w_{FP}. For a particular value of w_{FP} above 1, the dynamics are sensitive to the value of w_{PF}. All the regions on the parameter space can be accessed with the reported range of values for the three species of forb (w_{PF}: 1.32–0.25 and w_{FP}: 1.29–0.98) indicating that the results would not be robust to variation in the forb–parasite interactions. When the grass–parasite parameters are varied pairwise (Fig. 3c,d) over the range observed in this study (w_{PG} approximately 3 to 5, $w_{GP} < 1$) then changes in the parasite–grass interaction do not change the dynamics at any particular treatment. However, the low N and high N difference has a big overall impact on the expected dynamics due to the differences in the forb–parasite interactions between the two treatments.

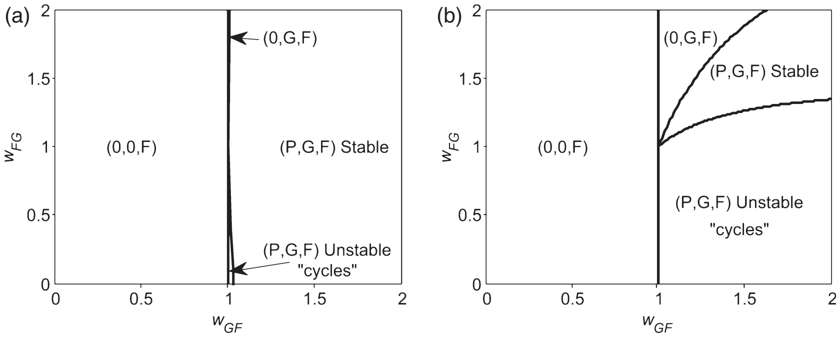

Fig. 2. Phase diagrams showing the effect of varying the magnitude of the grass–forb interaction (w_{GF}, w_{FG}) on population dynamics under low (a) and high (b) nitrogen. The equilibrium states of the three components are in parentheses (*P*, parasite; *G*, grass; *F*, forb), with zeroes indicating extinction of the respective component. The three-species equilibria are either stable or unstable; other equilibria are stable. See text for further explanation.

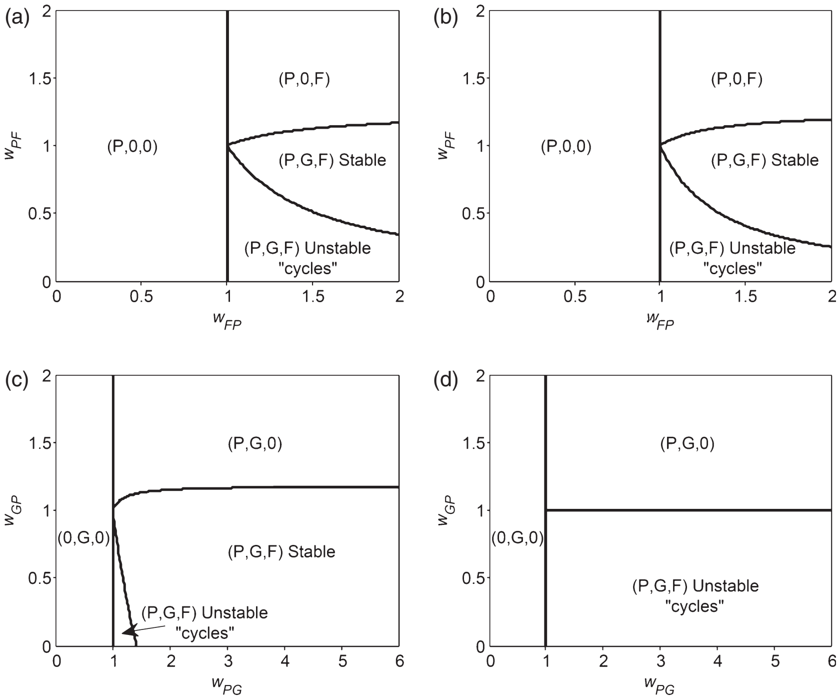

Fig. 3. Phase diagrams showing the effect of varying the magnitude of the forb–parasite interaction (a, b) and varying the parasite–grass interaction (c, d) on population dynamics under low (a, c) and high (b, d) nitrogen. The equilibrium states of the three components are in parentheses (*P*, parasite; *G*, grass; *F*, forb), with zeroes indicating extinction of the respective component. The three-species equilibria are either stable or unstable; other equilibria are stable. See text for further explanation.

SPATIAL MODEL

With parameters from the high N experiments, the outcome of the spatial model depended on the starting conditions. If the community components were equally distributed in space and started at approximately the same frequency, then the outcome was highly unstable and closely resembled the outcome from the non-spatial dynamics. However, when the populations were started with predominantly grasses and forbs at approximately equal frequencies and the parasitic plants were introduced from one edge of the arena, the community dynamics stabilized and all three functional types (grass, forb and parasite) were maintained in the population (Fig. 4). There were long-term oscillations in the abundance of the three components, in a regular round-robin fashion with a peak in the frequency of grass being followed by one in the parasite and then in the forb, but with some variation over time in the magnitude of the oscillations (Fig. 4).

With parameters from the low N experiments, as expected (given the asymptotic stability of the within-population dynamics), spatial structure had relatively little impact on the outcome if the population was started close to the equilibrium frequencies (not shown). Spatial structure did result in a somewhat higher frequency of the grass and the parasite, than in the unstructured deterministic case. If the starting frequencies were relatively far from equilibrium, there was frequently stochastic extinction of the grass component.

The non-spatial model presented above is deterministic, while the spatial model is stochastic. To more clearly pinpoint if the effects seen here were due to spatial structure, we also

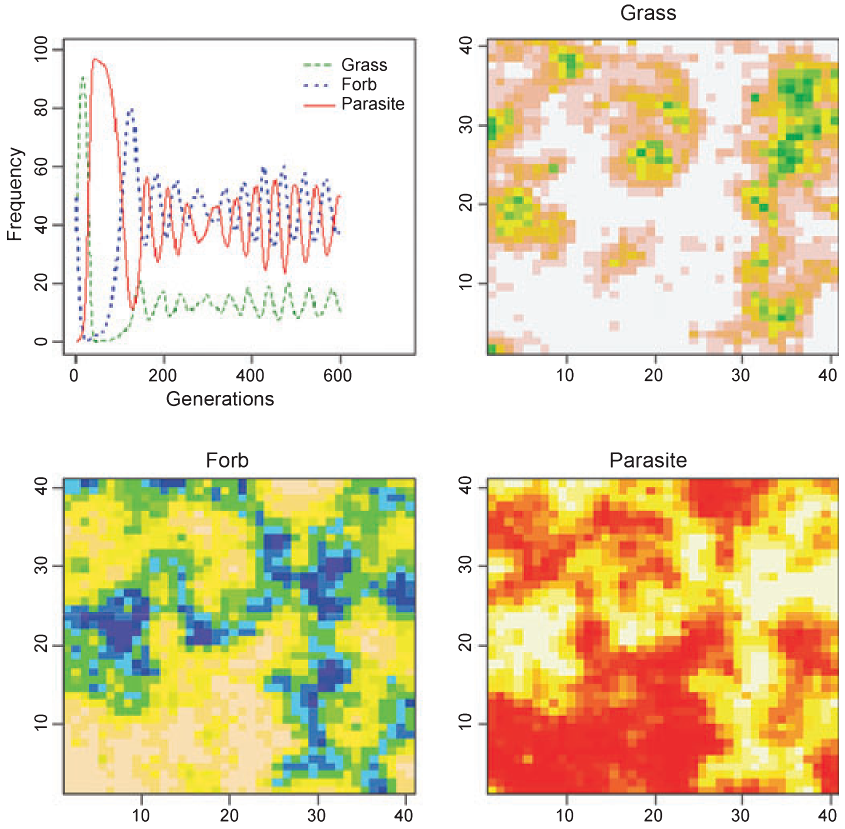

Fig. 4. Temporal population dynamics and surface view of spatial structure of a parasite–grass–forb community at steady (i.e. ergodic) state after *c.* 500 generations. Parameters are for interaction coefficients in high nitrogen (see Table 1). In the spatial maps high abundance of grass is green, high abundance of forb is blue and high abundance of parasite is red. The parasitic plant was introduced at a frequency of 0.33 in one corner of the lattice (grid locations 1, 1 to 1, 20); in the rest of the grid there were equal numbers of grasses and forbs. Migration among cells, $m = 0.2$; long-distance migration $m' = 0.01$; $K = 100$. x- and y-axes in the grass, forb and parasite sections represent coordinates in the spatial plane.

investigated a stochastic version of the non-spatial model. In the stochastic model, numbers were calculated from predicted frequencies after species interactions, but using binomial sampling from a population of the same size as the sum of the individual carrying capacities ($K = 100$) of the cells (40×40) in the spatial arena. Within the parameter ranges investigated, the differences we found between the two non-spatial and spatial models were largely due to the effects of spatial structure. With high-nutrient parameters, stochasticity *per se* always reduced rather than extended the coexistence times. Under low-nutrient parameters, stochasticity made coexistence less likely as low population sizes tended to lead to extinction of the grass, especially if populations were started away from the equilibrium state. However, when equilibrium was reached, the stochastic version of the non-spatial model resulted in oscillations among the components (Fig. 1c). This cycling has the superficial appearance of being deterministic, but is absent from the deterministic version of the same model; it is actually the result of stochastically induced resonance, a phenomenon observed generally in systems described by a set of non-linear equations and occurs even at large population sizes (Alonso, McKane & Pascual 2007).

We investigated whether the dynamics that would be observed were dependent on the size of the sampling unit used (as might occur for example in a field study where quadrat size is varied), by running the simulation on a large arena, but then sampling a smaller quadrat within this arena (Fig. 5). When the sample area was smaller, the fluctuations were of a higher amplitude; however, the effect on the frequency of the oscillations appeared to be relatively small, although we did not investigate this thoroughly. The sequence of peak abundances of the three components was the same at all sampling scales.

Discussion

> it may be impossible, much to the chagrin of 'niche theorists' to speak, even in principle, of the equilibrium point of a community – Gilpin (1975).

The major functional components in our experiments were parasitic plants (specifically the hemiparasite *R. minor*), grasses and forbs. Our pairwise competition experiments showed that parasitic plants reduce the performance of grasses, but that forbs outperform parasitic plants (see also Cameron 2004; Cameron *et al.* 2005, 2008; Cameron, Coats & Seel 2006). Although the grass versus forb pairing was missing in our experiments, a reasonable assumption is that grasses will outcompete forbs (Del-Val & Crawley 2005). If grasses generally outcompete forbs then the outcome is a series of intransitive relationships among the three components, analogous with those predicted by Smith (2000). The community dynamics of parasitic plants can therefore be conceptualized as a three-component system that has the dynamical features of classical 'rock–paper–scissors games'. There are two features of such dynamical systems that are relevant to understanding parasitic plant communities.

First, relatively small shifts in parameter values can result in qualitatively different dynamical outcomes (May & Leonard 1975). There may be convergence to a stable equilibrium and coexistence of all three components, as seen in our model using

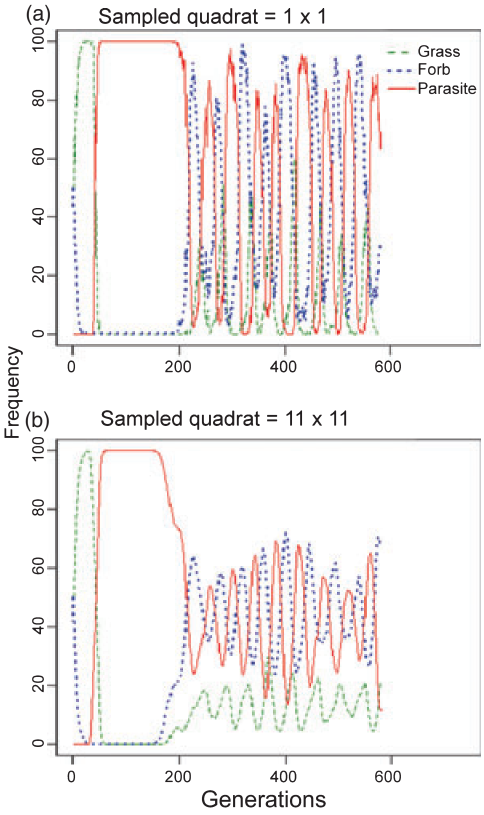

Fig. 5. Temporal dynamics observed if data is taken at (a) 1 × 1, (b) 11 × 11 quadrat scales. Results shown are for a typical run for interactions under high nutrients, with parameters as in Fig. 2.

parameters for low-nutrient conditions. Alternatively, the components may show cycles of ever-increasing amplitude, and this occurred in our study for the parameters obtained under high-nutrient conditions. In the latter case, in any biologically realistic system where fractional individuals are impossible (and stochastic processes are present), one of the types is eventually lost when it reaches an extreme low frequency. Which type will be lost is again very unpredictable, in the sense of being sensitive to both starting conditions and stochasticity. To better understand the range of outcomes, we carried out stability analyses on our model (Appendix S1). Stability analyses on three-species interactions, using an ordinary differential equation framework and in a more abstract context, were carried out by May & Leonard (1975) and Gilpin (1975), based on the Lotka–Volterra competition equations. Our model has no particular virtues other than its simplicity and its direct connection with data from the pairwise competition experiments. However, by connecting it to such data, it can be shown that the outcomes are not 'all chaotic'. For example, even though we had to make assumptions about the forb–grass interaction (as it was not included in the experimental treatments), the analysis showed that the qualitative outcome was insensitive to the magnitude of this interaction, providing grasses outcompeted forbs in a relatively reciprocal way. Grasses generally outcompete forbs in grassland communities (Del-Val & Crawley 2005), but there are clear cases where this does not hold given there are some highly competitive species of forb. Instead, the outcomes were particularly sensitive to the nature of the forb–parasite interactions, and the predicted difference in the dynamics under the two N regimes was because of an effect of N on this interaction. Moreover, because (even within N treatments) there was large variation among forb species in their interaction with the parasite, forb resistance may be the key driver of the dynamics. It is not known whether the community outcomes would be correctly predicted by averaging individual species values, because this requires the assumption that the interaction effects are additive. However, such additivity is readily testable by further experiments.

A second major feature of rock–paper–scissors systems is that even if the interactions are locally unstable, they can be stabilized by spatial sub-structuring (Durrett & Levin 1997; Kerr *et al.* 2002; Reichenbach, Mobilia & Frey 2007). Our results were in complete agreement with these findings, including the observation that the level of stability of the spatial system depends both on the initial frequency and also on the initial spatial pattern or distribution of the interacting components. Thus, we showed that if the parasitic plant is started throughout the arena at low frequency (analogous to sowing seeds of the parasite into a meadow community), the outcome is cycles of large amplitude, whereas if it is started at one edge of the arena (analogous to the parasite invading new territory), there are local cycles but overall general stability. Similar effects of initial starting conditions have been seen in spatial simulations of other interacting species (e.g. parasitoids, Comins, Hassell & May 1992).

Experimental and field studies have shown that parasitic plants substantially influence the structure and functioning of the plant communities they inhabit (Ameloot, Verheyen & Hermy 2005). In spite of this, the effects of the parasite on host community structure are very variable and the dynamics of hemiparasites and their hosts remain highly unpredictable in field situations (Ameloot, Verheyen & Hermy 2005; Cameron *et al.* 2005). Hemiparasites can promote species diversity if they successfully attach to the dominant species freeing sub-dominant species from competitive exclusion (Gibson & Watkinson 1992). For example, Marvier (1998) showed that the forb *Hypochaeris glabra* was freed from competition with the grasses when the root hemiparasites *Triphysaria pusilla* and *eriantha* were present. Additionally Pennings & Callaway (1996) and Callaway & Pennings (1998) showed that the shoot holoparasite *Cuscuta salina* can influence the structure of salt marsh communities by preferentially parasitizing *Salicornia virginica* and therefore allowing less-preferred *Limonium californicum* and *Frankenia salina* to proliferate. These shifts in host community structure have long been assumed to be caused by selective parasitism of 'preferred hosts' (Gibson & Watkinson 1992), and there is good evidence for host preference in some parasitic plants such as the stem holoparasites *Cuscuta* spp. (Callaway & Pennings 1998). However, in the case of *R. minor* no active host selection has been observed. Gibson & Watkinson (1992) suggested that *R. minor* chooses *Plantago lanceolata* as a preferred host, yet subsequent studies showed that although the parasite forms haustoria on this species, it cannot access any of the host's resources (Cameron & Seel 2007) and indeed that this association may even be lethal for the parasite (Cameron, Coats & Seel 2006). Recent evidence has suggested that the higher resistance (or tolerance) of the forbs to parasitic attack relative to the resistance of grasses drives parasite-induced shifts in host community structure rather than selective parasitism that is highly species-specific (Cameron *et al.* 2005; Cameron, Coats & Seel 2006; Cameron & Seel 2007; Rümer *et al.* 2007; Westbury & Dunnett 2007).

The simulations presented here were not designed to be realistic representations of any particular plant community. Furthermore, the parameters used in the simulations were based on simplified pairwise pot experiments (albeit using seed from naturally co-occurring species). Nevertheless, these simplified experiments and models have several important general implications for future, more detailed studies of these systems as well as for the management consequences of introducing parasitic plants into communities with the goal of sustaining biodiversity. First, it is clear that to explain the coexistence of parasitic plants and their hosts, it is not necessary to invoke what can be broadly termed 'niche partitioning'. In our study, the pairwise interactions were almost completely reciprocal, and in no case did they lead to pairwise coexistence. Coexistence in low-nutrient treatments was maintained by intransitive interactions, and in high-nutrient treatments by the spatial restriction of such interactions. We did not model resources (or density dependence explicitly) and this would be interesting to do, especially as Smith (2000) showed that co-existence is possible between a hemiparasite and its host, even when they compete for identical resources. Therefore, while niche partitioning cannot be excluded as a factor in any real-world situation, it is not a *necessary* feature for the stability of plant communities with hemiparasites.

Another characteristic of rock–paper–scissor interactions is that in spatial models there are continuing local cycles (Reichenbach, Mobilia & Frey 2007). Indeed, coexistence by shifting clouds of locally unstable interactants was observed in the simulations. The amplitude of the oscillations decreased as the size of the sampling unit increased, but it was surprising that in our study the frequency of the oscillations seemed relatively unaffected over a broad range of sampling scales. Whether this is a peculiar outcome of the particular parameter values that were used, or is a 'signature' feature of rock–paper–scissors dynamics deserves further investigation.

The distribution of the parasite across the community is likely to determine the impact parasitic plants have on their communities. Our simulations show that introducing parasitic plants in one corner of a plot (analogous to the invasion of a community by the parasite from an adjacent, infested plot) may produce very different outcomes from introducing them uniformly throughout the plot (analogous to the establishment of a new meadow community from seed or the sowing of parasitic plants into an extant community). This is an expectation that is highly amenable to field experiments, but we know of no study that has tried to test this idea.

The results of both the simulations, especially so under low-nutrient conditions, predict an unrealistically low representation of grasses for the types of community in which *R. minor* is found (Hwangbo 2000). The precise reasons for this are unclear. The experiment was carried out over 14 weeks and allowed no period of 'recovery' after seed set and death of *R. minor*, perhaps over-emphasizing its effect on perennial grasses that can recover during the winter months. However, Seel & Press (1996) showed significant negative 'legacy effects' of the parasite on the performance of the perennial grass *Poa alpina* 1 year after the removal of the parasite. Moreover, our model did not take into account likely life-history differences between the community components, but assumed turnover rates of all three components were identical. In the absence of field-based demographic data, simulations adding life-history effects would have required choosing parameters essentially by 'guesswork'. However, approaches incorporating more realistic life-history features could be very productive and informative, if linked to a specific empirical system and combined with experimental field studies.

Despite the fact that our simulations were not designed to be realistic representations of any particular plant community, there are striking similarities between the dynamics that emerge from these simulations and the observations of the effect of *R. minor* on host community structure and dynamics under field conditions. Ameloot, Verheyen & Hermy (2005) undertook an extensive meta-analysis investigating the general trends in *R. minor*-induced shifts in host community structure. Across 21 studies, that there was a 56% suppression of the grasses and a 16% increase in the forbs, a trend observed in both the long and short term (Ameloot *et al.* 2006) and consistent with the shifts in community structure predicted by our study. Moreover, field studies have shown that the communities that *Rhinanthus* inhabits are spatially and temporally dynamic (Kelly 1989). As the parasite suppresses the biomass of its 'preferred' host (*sensu* Gibson & Watkinson 1991), its own abundance will decline as the 'preferred' host becomes limiting (Pennings & Callaway 2002). This also led Cameron (2004) to suggest that the grassland community exists as a mosaic of contiguous patches oscillating between forb-rich and grass-rich phases. Further, de Hullu, Brouwer & ter Borg (1985) observed oscillations in the percentage cover of *Rhinanthus angustifolius* over time. The abundance of the parasite rapidly increased after a change in management of the grassland community from an intensive regime unfavourable for the parasite to a less-intensive regime (de Hullu, Brouwer & ter Borg 1985), parasite abundance then later declined, presumably as a function of localized host depletion. In addition, de Hullu, Brouwer & ter Borg (1985) showed that the abundance of *R. angustifolius* was cyclical over time, alternating between parasite-rich and parasite-poor phases as predicted by our model. In direct support of our predictions of instability of *R. minor* populations under conditions of high nutrient supply, field studies have shown that *R. minor* populations can be highly unstable in highly productive grasslands and may fail to establish in the long term (Westbury *et al.* 2006).

There is growing interest in the role of parasites in determining not only community structure but also ecosystem functioning. Lafferty *et al.* (2005) have shown that macroparasites in salt marsh communities not only form a large proportion of the biomass (often exceeding that of higher trophic levels), but that they also greatly increase the number of linkages in the food web. In animal communities, parasites with alternate hosts can also lead to unusual intransitivities, which can transform apparently ‘parasitic’ relationships into ones with more mutualistic outcomes (Lafferty 1992). Parasitic plants, especially hemiparasites, also demonstrably affect the species composition and productivity of their communities (Ameloot *et al.* 2006). Because of their visibility and experimental tractability, parasitic plants will remain important empirical models for understanding how other less-visible parasites and pathogens might also influence community structure and functioning.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Steady state and stability analysis.