

Spatial and temporal dynamics of insect outbreaks in a complex multitrophic system: tussock moths, ghost moths, and their natural enemies on bush lupines

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To understand the spatial and temporal behavior of outbreaks, it may be necessary to go beyond simple plant–herbivore dynamics and consider trophic complexity, environmental heterogeneity, limited dispersal, and their possible interactions. We examine many of these factors in a system consisting of one plant, two insect herbivores, and multiple natural enemies. Bush lupines (*Lupinus arboreus*) in coastal California support intense but spatially localized outbreaks of the tussock moth (*Orgyia vetusta*), a flightless defoliator. Bush lupines are also attacked by the stem-boring larvae of the ghost moth (*Hepialis californicus*), which may cause periodic mass dieoffs of lupine stands. Here we extend previous models of the tussock moth and its natural enemies to include changes in the carrying capacity (i.e., lupine abundance) caused by the ghost moth and its primary natural enemy. By superimposing these two strongly interactive subsystems, we generate new questions and predictions.

Introduction

Many explanations have been put forward for the spatial and/or temporal behavior of herbivorous insect populations. Some of these explanations primarily emphasize extrinsic variation in host-plant quality or abiotic conditions (e.g. Haukioja 2005, Mopper 2005, but see Gripenberg & Roslin 2005), while others emphasize the intrinsic dynamics of the interactions of the outbreking herbivores with either their host plants or their natural enemies (e.g. Denno *et al.* 2005, Roland 2005). For the most part, studies of out-

breking insects — those which, by definition, show high temporal variation in abundance — either do not attempt to explain spatial variation, or assume that such variation is due to the external environment. Yet many or most outbreking insects also show striking variability in space (e.g., Furniss & Knopf 1971, Mason & Luck 1978, Wickman & Beckwith 1978, Mason & McManus 1981, Berryman 1987, Harrison 1987, Watt & Leather 1990, Nair 1990, Hunter *et al.* 1991), and the causes of spatial variation may be dynamic rather than static (e.g., Bjornstad *et al.* 2002). Very few studies have jointly considered

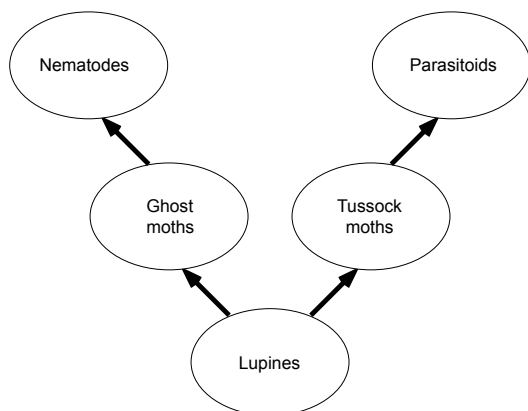


Fig. 1. The food web examined in this study.

the spatial and temporal behavior of outbreaks, nor attempted to consider both the extrinsic and intrinsic processes that may be responsible.

If the spatio-temporal dynamics of outbreaks involve higher-order interactions among many or all of the above-mentioned factors — such as weather, fixed spatial variation in the environment, host-plant quality, predation, perhaps even competition — then understanding their complexity may lie just beyond the reach of most models and empirical studies alike. Here we present a case study that we believe illustrates this proposition. After more than a decade of empirical and theoretical study by two research groups, we are beginning to understand two strongly interactive subsystems within a single study system that consists of one plant, two herbivores, and several natural enemies (Fig. 1) in a spatially and temporally varying environment. Our goal here is to begin examining the complex ways in which this moderately large number of elements may interact to determine population trajectories.

Bush lupines (*Lupinus arboreus*) are one of the most common shrubs in the dunes and grasslands of coastal California, including at our main study site, the University of California's Bodega Marine Reserve. They often occur in monodominant stands covering hundreds of acres, although they occur in smaller and mixed stands as well. Their prolific N-fixation has dramatic effects on the coastal ecosystem (Maron & Jefferies 1999). The bushes produce prolific quantities of seed but most of it is consumed by insects and rodents

(Maron & Simms 2001). Adult bushes host a rich fauna of insect herbivores. Individual bushes typically live less than ten years, and stands of thousands of bushes are sometimes observed to die simultaneously (Strong *et al.* 1995).

Outbreaks of tussock moths (*Orgyia vetusta*) can lead to the near-total defoliation of lupine stands at our study site, and may last for several years. As described in more detail below, we now understand the role of parasitoids in controlling the spatial (but not the temporal) behavior of tussock moth outbreaks on lupines. Ghost moths (*Hepialus californicus*), whose larvae feed within plant stems, are less conspicuous but deadlier insect herbivores of bush lupines. As described below, we are now beginning to understand how the interaction of ghost moths with their principal natural enemy may affect the temporal dynamics of lupine stands, and in turn, how this interaction may link lupine stand dynamics to the El Niño/Southern Oscillation (ENSO) rainfall cycle.

We will first describe in more detail the empirical and modeling work on each of these subsystems and discuss the main unanswered questions about each one. We will then present a model that integrates the two subsystems, and use this model to pose new questions and generate new predictions about the complex behavior of the system as a whole.

Lupines, tussock moths, and parasitoids

Empirical work on spatial variation in moth density

The western tussock moth (*Orgyia vetusta* Bdv., Lymantriidae) is a generalist forest defoliator, but in the dunes and grasslands of the California coast it feeds almost exclusively on perennial lupines (*Lupinus arboreus* Sims in the north and *L. chamissonis* Eschs. in the south). The moth may achieve densities at which larvae completely defoliate lupine bushes, and may maintain such densities at a single site for multiple consecutive years.

Searches of the California coast in 1996 found four dense populations of the tussock

moth, each inhabiting tens to hundreds of bushes within lupine stands that numbered in the tens of thousands (Harrison 1997). Variable host-plant quality did not appear to play a role in restricting outbreaks; moths reared from hatching to pupation on bushes inside and outside the outbreak areas at the four sites showed equal survival, pupal weight and development time (Harrison 1994, 1997). The abundances of generalist predators, such as ants and spiders, also did not differ between outbreak and non-outbreak areas (Harrison & Wilcox 1995, Harrison 1997).

The adult females of this moth are flightless, and limited mobility appears to play a role in the spatial restriction of tussock moth outbreaks. In two experimentally created outbreaks at Bodega, the median displacement of moths after one complete generation was only two meters from the release point (Harrison 1994). While newly hatched larvae can disperse by aerial "ballooning", they did not appear to balloon in response to previous-year defoliation or starvation (Harrison 1995).

A density-manipulation experiment showed that the outbreak population was strongly food-limited (Harrison 1994). Nonetheless, defoliation seldom killed the host plants, and heavily attacked plants recovered their biomass and seed production fully within one growing season (Harrison & Maron 1995). Experiments also showed that tussock moths on lupines did not suffer delayed density dependence through long-term reductions in food quality (induced defenses) or larval quality (maternal effects), in contrast to some other outbreaking insects (Harrison 1995).

Parasitoids of the tussock moth at Bodega are all locally specialized on the moth. They include the scelionid wasp *Telenomus californicus* Ashmead, which parasitizes eggs, and three tachinid flies that attack larvae and emerge from pupae: *Tachinomyia similis* Williston, *Patelloa pluriseriata* or *fuscimacula* Aldrich and Webber, which inserts its eggs into the larva; and *Protodejeania echinata* Townsend, which oviposits on host plant foliage.

Brodmann *et al.* (1996) placed groups of tussock moth eggs or larvae on bushes within the outbreak area, and along a transect emanating 500 m from its edge through suitable but unoccupied habitat. Parasitism by all the above species

was significantly higher just outside than inside the outbreak, e.g., 6% inside versus 14% outside for *Telenomus*, and 25%–35% inside versus 40%–60% outside for *Tachinomyia*. Parasitism by most species followed a parabolic relationship with distance from the outbreak, peaking at 100–200 m from its edge, although parasitism by *Tachinomyia* increased monotonically with distance from the outbreak (Brodmann *et al.* 1996).

Maron and Harrison (1997) created small experimental outbreaks by placing 1000 newly hatched moth larvae on 44 lupine bushes at distances of 0–700 m from the edge of the outbreak. To examine the possible role of ground-dwelling predators, these bushes were surrounded by either 30-cm fences topped with Tanglefoot®, or control fences with four 10-cm wide gates. The survival of moths to the pupal stage was substantially higher farther from the natural outbreak, and the numbers of parasitized larval corpses found beneath the bushes showed the opposite trend (Fig. 2). Numbers of egg masses produced by surviving moths also increased strongly with distance from the edge of the outbreak. The experimental populations were completely suppressed at distances up to 200–300 m from the natural outbreak, while at greater distances, net population growth was nearly always strongly positive. Although predator exclusion affected the survival of first and second-instar larvae, it did not significantly affect the numbers of egg masses per bush, showing that distance-dependent parasitism overwhelmed the initially strong effect of predation (Maron & Harrison 1997).

Theoretical models of spatial pattern formation

These experimental results from the tussock moth population are consistent with a longstanding idea in the theoretical literature, namely that spatial patterns in population density can arise from the interaction between a predator and prey (or host and parasitoid) with different levels of mobility. Such theory was originally based on reaction-diffusion models that portray a predator and prey "reacting" according to Lotka-Volterra or similar continuous-time dynamics, and "diffusing" by moving randomly through

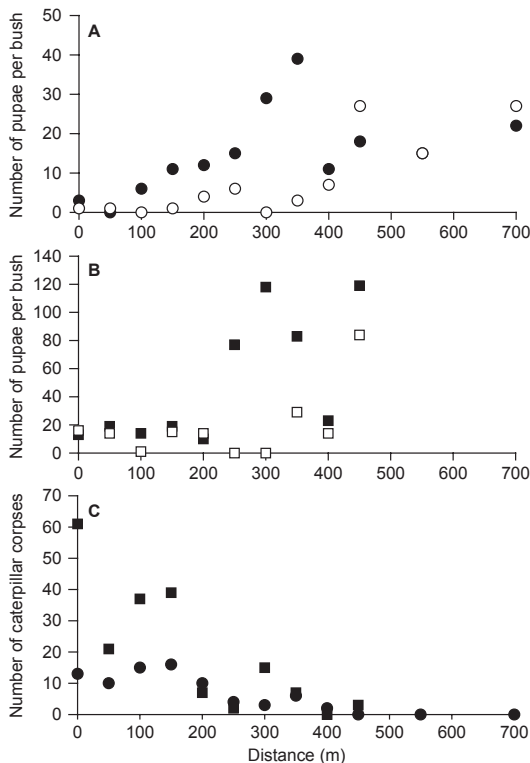


Fig. 2. Field results from the tussock moth system: effect of distance from the edge of the natural tussock moth outbreak on the number of caterpillars surviving to pupation within experimental outbreaks established on single lupine bushes in (A) grassland and (B) dune habitats; and (C) the numbers of parasitized caterpillar corpses found under these experimental lupine bushes in both habitats. Open symbols: bushes exposed to generalist ground-based predators; filled symbols: bushes protected from such predators. From Maron and Harrison (1997).

continuous space (e.g. Mimura & Murray 1978, Deutschmann *et al.* 1993, McLaughlin & Roughgarden 1993, Holmes *et al.* 1994, Lewis 1994, Neubert *et al.* 1995, Turchin *et al.* 1997). Two basic assumptions are that the interaction is strong, i.e., the natural enemy must be capable of reducing its victim's abundance and increasing its own abundance in response to that of the victim; and that the natural enemy must disperse substantially faster than its victim.

In these models, a localized patch of prey population that arises for random reasons leads to corresponding spatially-localized growth in the predator population. Because it is faster dispersing, the predator spills over the edges of the patch of prey, creating a peripheral zone

in which predator-to-prey ratios are elevated. In turn, this effect locks the patch into place, because prey that disperse out the patch suffer a high risk of being eaten. Within the patch, the prey is saved from annihilation by the constant diffusive loss of part of the predator population. The result is the formation of standing waves in the densities of both species through space, with a wavelength determined by the predator's dispersal abilities.

Hastings *et al.* (1997) adapted the model of Conway (1984) to the specific case of the tussock moth and its parasitoids. Host and parasitoid populations grow in continuous time and disperse in continuous space. Their dynamics include a host carrying capacity set by resources and a saturating functional response in the parasitoid. The parasitoid disperses by random diffusion within a bounded one-dimensional environment, while the host is assumed to be nearly immobile. Hastings *et al.* (1997) use a singular perturbation technique to show that under these assumptions, there exists a stable spatial solution that exhibits a "jump" from high host density to zero host density, with the location of this jump jointly determined by the population dynamics of both species and the dispersal ability of the parasitoid. One counter-intuitive behavior of this model is that host density reaches its highest level just before the point in space where it drops to zero, a pattern that is matched by data from the tussock moth system (Hastings *et al.* 1997).

In further elaborations of this work, Wilson *et al.* (1999) showed that an individual-based model reflecting detailed features of the tussock moth system gives qualitatively similar results to the simple discrete-time analytic model of pattern formation, and McCann *et al.* (2000) showed that spatial pattern formation can arise in an analytic model with discrete space as well as discrete time. Importantly, McCann *et al.* (2000) demonstrate that predator dispersal does not have to be completely random; spatial pattern can arise even with moderate levels of aggregation by the predator toward the prey. Likewise, Holmes *et al.* (1994) suggest that, although strong aggregation of predators toward their prey will annihilate spatial pattern, a weak (undercompensating) tendency for predators to aggregate to prey could promote pattern formation.

Unanswered questions

One limitation of the models of spatial pattern formation is their assumption that predators disperse by random diffusion. More realistic mechanisms are needed to explain, first, why predators fail to suppress the prey population, and second, why they move away from dense concentrations of their prey to the extent necessary to prevent the expansion of the prey population. One strong candidate is mutual interference among parasitoids, which could both lower their efficiency and cause some degree of disaggregative movement. However, an experimental study by Umbanhowar *et al.* (2003) did not find evidence for mutual interference in the fly parasitoids of the tussock moth. Alternative possibilities are that slow and time-lagged population growth explains the lack of immediate suppression of the moth outbreak by the flies, and that a small amount of random movement explains the occurrence of flies outside the outbreak area.

Another unanswered question is whether spatial pattern formation can (and does) occur in the absence of external environmental variation, or whether it acts by reinforcing such variation, as suggested in theoretical work by McLaughlin and Roughgarden (1993) and Keitt *et al.* (2001). Two observations suggest that in the tussock moth system, host–parasitoid interactions serve to amplify the effect of underlying environmental gradients. First, in dune habitat, the survival of moths on experimental bushes > 200 m from the outbreak was several-fold higher than in grasslands, and dunes have sparser lupine bushes (Brodmann *et al.* 1996) and lower densities of generalist predators (Harrison & Wilcox 1995). Second, lupines appear to be longer-lived within the natural outbreak area than elsewhere, which may reflect variation in the natural enemies of the ghost moth (Strong *et al.* 1995).

Finally, it is unclear from existing theory how spatial pattern formation should interact with temporal dynamics. In the case of herbivorous insects and their parasitoids, it is reasonable to expect that variation in weather and resource (host plant) supply should constantly perturb the equilibrium patterns in density predicted by spatial models. As the prey carrying capacity changes, for example, it is unclear whether the

discrete patches of prey population should contract and expand in space, or rise and fall *in situ*. We will address this question below, because of its particular relevance to tussock moths feeding on lupine bushes that are also attacked and periodically killed by ghost moths.

The lupine, ghost moth, and nematode system

Another powerful foodweb module in this system leads from the lupine through root feeding insects to entomopathogenic nematodes and forms a powerful trophic cascade. Ghost moth caterpillars are by far the most abundant root feeders in the system. Bush lupine alone supports this population of herbivores. The moths are strong flyers and deposit eggs widely over the extent of the local lupine populations at Bodega Head and nearby Point Reyes. In high density years, their caterpillars bore the roots of virtually every large lupine bush on Bodega Head. Even at low densities, they kill a small proportion of lupine bushes (Maron 1998). Higher densities result in substantially lowered growth rates and seed set (Preisser 2003), and yet higher densities kill a large fraction of bushes (Strong *et al.* 1999).

Entomopathogenic nematodes attack the root feeding ghost moth caterpillars. These nematodes are obligate insect enemies of soil and litter (Hominick 2002) with the potential to cause high mortality to host populations (Strong *et al.* 1995, 1996). Adults, reproduction, and feeding of entomopathogenic nematodes are restricted to the interior of host insects. The nonfeeding infective juveniles, or third-instar larvae, live in the soil, search for and kill hosts, and disperse. An infective juvenile enters the insect host through a spiracle or other orifice, punctures a membrane, then regurgitates a mutualistic bacterium that quickly kills, digests, and preserves the host with antibiotics. The bacterial population provides food for the exponentially growing nematode population inside (Strong 1999). In the lupine system on the California coast, *Heterorhabditis marelatus* is the most abundant entomopathogenic nematode. Species in this family are hermaphroditic, and a single infective juvenile will kill a large ghost moth caterpillar to produce hundreds of thousands of propagules.

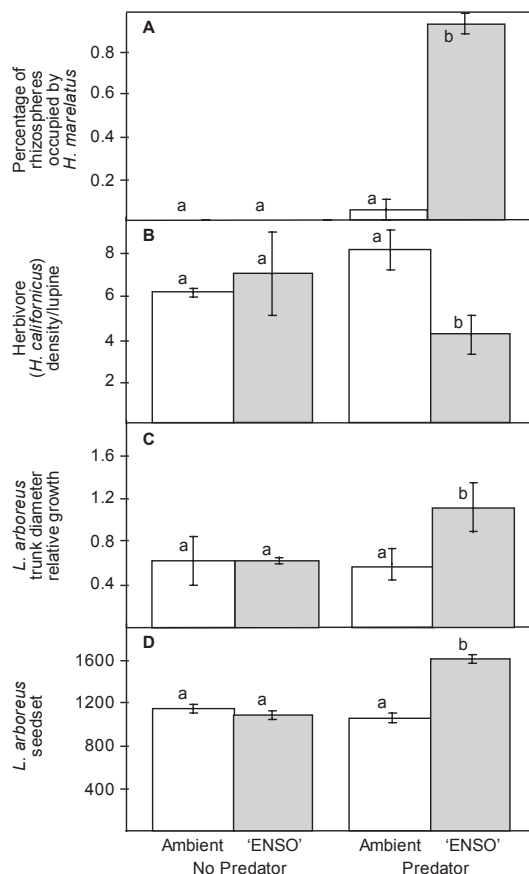


Fig. 3. Field results from the ghost moth system: effect of watering treatment (ENSO-mimicking or ambient) and nematode addition treatment (predator added or no predator added) on (A) nematode persistence, (B) ghost moth presence, (C) lupine trunk diameter growth, and (D) lupine seedset. Bars represent the means of two plots/treatment taken from ten bushes/plot, and error bars are one standard error of plot means. Lowercase letters indicate statistically different means at $P < 0.05$ (Student's t -test). From Preisser and Strong (2004).

The first evidence of a trophic cascade in which *H. marelatus* protects bush lupine from ghost moth caterpillars was found in a decade-long inverse correlation between incidence of the nematode and bush lupine mortality over the 125-hectare landscape of Bodega Head (Strong *et al.* 1995, 1996). A field experiment showed that while seedling survival decreased exponentially with increasing densities of early instar ghost moth caterpillars, the presence in low density of *H. marelatus* canceled the lupine

mortality caused by this root feeder (Strong *et al.* 1999). Considering large, mature lupine, *H. marelatus* halved densities of large ghost moth caterpillars, increased lupine trunk growth by 67% and increased seed set by 44% within one growing season (Preisser 2003).

The fascinating element of this food web module is that the manifest local success of the entomopathogenic nematode does not translate into general spatial success; while the host plant and host insect are ubiquitous in the study area, *H. marelatus* never occupies more than about 5% of the rhizospheres of bush lupine. Our earlier speculation that nematophagous fungi caused such high mortality to *H. marelatus* as to be the cause of its lack of success in occupying a larger fraction of the landscape (Strong 1999) has turned out to be incorrect (Jaffee & Strong 2005). Under conditions most favorable to nematode mortality, more than 70% of the hundreds of thousands of infective juvenile *H. marelatus* escape the fungi.

Years of low summer soil moisture of the Mediterranean climate probably play a substantial role in spatial restriction of this natural enemy. Experimentally increasing soil moisture to levels found in summers following the heavy rains of El Niño/Southern Oscillation (ENSO) winters leads to higher survival and persistence of *H. marelatus*, which suppressed an outbreak of the ghost moth caterpillar and indirectly protected the lupine (Preisser & Strong 2004; Fig. 3). Huge local populations of *H. marelatus* can occur in a single rhizosphere of lupine, as the product of a few large ghost moth hosts. Our current research is testing the idea that most interannually persistent local populations of *H. marelatus* occur in the fraction of the landscape providing the wettest summer soils and the most consistent host populations. During winter rains, *H. marelatus* disperses well beyond the range to which it retreats during the dry summer. Very little information is available about the mechanisms of dispersal of entomopathogenic nematodes, and we are testing the role of phoretic dispersal of *H. marelatus* on the exterior of terrestrial arthropods, which are immune to the nematode (Eng *et al.* 2005).

A fully stochastic model indicates the extreme sensitivity of this trophic cascade to variations in

summer soil moisture and concomitant effects upon survival of the entomopathogenic nematode. With the high survival characteristic of wet places and ENSO years across the landscape, the nematode is prone to overexploit its hosts and suffer subsequent local extinction. In dry conditions, survival falls so far that it underexploits hosts, which also leads to local extinction. Published rates of mortality suggest that nematode mortality is commonly high enough to lead to underexploitation. With a field survival experiment that ran much longer than previous experiments, we found that field mortality is lower than published values. These lower mortality rates mean that short-term over-exploitation did not lead to extinction because a subset of the cohort survived for several years within the rhizosphere. The long term survivors are present when the rhizosphere is recolonized by host insects in subsequent years. The lower mortality leads to long-term persistence of local nematode populations across a range of initial nematode densities.

The climatic variability of ENSO is the major evidence for tendencies toward cycling in the system. Higher soil moisture will lead to higher nematode survival. The resulting pulse of high lupine survival will dominate the age structure of host plants for a number of years.

The model

A complete model of the dynamics of the interaction among the species would require information we do not currently have. However, we can use a simplified model to explore one important aspect: how changes in lupine abundance caused by the ghost moth would affect the spatial dynamics of tussock moths and their parasitoids. This builds upon our earlier work (Hastings *et al.* 1997) which in turn relied upon the insightful work of Conway (1984) to develop a static view of the spatial patterns generated by the interaction between exploiter and victim, where the victim disperses at a much slower rate than the exploiter. In this earlier work we showed that a static outbreak pattern, with tussock moth abundance highest at the edge of the outbreak, resulted from an interaction between mobile, randomly searching parasitoids and their stationary hosts.

Analysis of spatial models such as these, using singular perturbation approaches that take into account the slow victim movement, is quite complex (Conway 1984). As is shown by the numerical calculations in Owen and Lewis (2001) for the typical predator-prey model with Type II functional response (which was the model used in Hastings *et al.* 1997) the stationary solutions with zero prey dispersal are not in fact the limit of stationary solutions with small prey dispersal, and instead slowly traveling waves result. Although for the time scales of our experimental work it would likely be impossible to distinguish between slowly traveling and stationary waves, we believe another approach is more fruitful.

As our earlier work (Maron & Harrison 1997, Hastings *et al.* 1997) discussed, the observed patterns appear to correspond to stable solutions with low prey densities inside the outbreak and high prey densities at the edge of the outbreak, corresponding to the solutions outlined by Conway (1984) for a subtly different predator-prey model incorporating density-dependence among the predators. We use Conway's (1984) model with predator interference, which he also shows can have stationary solutions. Owen and Lewis (2001) use very similar arguments to those of Conway (1984) to demonstrate that an Allee effect is another mechanism that can produce stationary patterns.

We equate changes in lupine abundance with change in the carrying capacity for the tussock moth, and ask how this affects the spatial pattern of moths and parasitoids, using the model with predator density dependence. The specific question we ask is: how does reducing the carrying capacity uniformly throughout the outbreak area affect the spatial distribution of moths and parasitoids? Specifically, does the spatial extent of the outbreak change, or does the population level within the outbreak change, or both? We examine this question using a model that is continuous in time and space, while recognizing that making one or both of these discrete might change some conclusions.

We follow the development in Conway (1984) closely. Let $u(x,t)$ be a density function on space for the tussock moth at time t , and $v(x,t)$ be a density function on space for the parasi-

toid at time t . Letting $f(u)$ describe the density dependent per capita growth rate of the tussock moth in the absence of the parasitoid, $g(v)$ the density dependent per capita death rate of the parasitoid in the absence of the tussock moth, and letting $\phi(u)$ describe the functional response of the parasitoid, we arrive at the model

$$\begin{aligned} u_t &= d_1 u_{xx} + uf(u) - uv\phi(u) \\ v_t &= d_2 v_{xx} - vg(v) + uv\phi(u) \end{aligned} \quad (1)$$

which has already been non-dimensionalized so that the parasitism term is the same in both equations. Here d_i is a diffusion coefficient for each species, and subscripts indicate partial derivatives. We also assume zero-flux boundary conditions, meaning that no moths or parasitoids enter or exit the system as a whole, which seems to be a reasonable assumption for the field system at Bodega Marine Reserve. Thus

$$u_x(-L) = u_x(L) = v_x(-L) = v_x(L) = 0 \quad (2)$$

which corresponds to the assumption that no individuals leave the one dimensional habitat of length $2L$. Our goal is to examine the response of steady state solutions of Eqs. 1 and 2 to changes in the function f .

We will use an argument appropriate to the lack of mobility of adult female tussock moths by looking for solutions that assume that d_1 is much less than d_2 . In fact, we use the singular perturbation approach outlined in Conway (1984), to look at solutions in the limit as d_1 approaches 0. Steady state solutions with $d_1 = 0$ will satisfy

$$\begin{aligned} 0 &= uf(u) - uv\phi(u) = u\phi(u)[h(u) - v] \\ 0 &= v_{xx} - vg(v) + uv\phi(u) \end{aligned} \quad (3)$$

which implicitly defines the function h . (Without loss of generality, we can assume here that $d_2 = 0$.) We assume a Type II (linear) functional response, so the isocline for the tussock moth has a hump. Thus from Eq. 3, if we solve for the isocline, we must solve

$$0 = h(u) - v$$

We let

$$u = k(v) \quad (4)$$

be the equation for the part of the host isocline that is to the right of the hump. We then look for solutions that correspond to an outbreak, meaning that in part of the habitat the tussock moth population satisfies Eq. 4 and in the rest of the habitat it is absent ($u = 0$). We then use these two possible tussock moth values in the parasitoid equation in Eq. 3 to obtain two equations for the parasitoid spatial density,

$$v'' - vg(v) = 0 \quad (5)$$

and

$$v'' + K(v) = 0 \quad (6)$$

where $K(v) = -vg(v) + k(v)\phi[k(v)]v$.

The idea is to look for an outbreak solution, which will satisfy Eq. 5 in part of the domain and Eq. 6 in the rest of the domain. These will be joined at an interior layer (Fife 1976) at which v and v' will match. There will be a unique choice of v , v' , and spatial location x_0 at which this match can take place; this can be the limit of a solution of Eq. 3 when the diffusion rate d_1 of the host approaches zero (Conway 1984), in the case where the spatial domain is divided into just two pieces: one corresponding to Eq. 5 and one to Eq. 6. A similar approach was used by Owen and Lewis (2001) to demonstrate that without predator density dependence the transition could only take place near the edge of the region.

One can start with the equations that describe this 'matching' condition, and ask how changing f — specifically, reducing the value of f to represent a reduction in the carrying capacity for the tussock moth — will change the value of v , v' and x_0 at which this match takes place. Using Eq. 4, this also gives information about how the level of the tussock moth population, u , is changed. A long but relatively straightforward argument using both graphical methods and implicit differentiation of the matching conditions (which will be published elsewhere) can be used to show that reducing the carrying capacity of the tussock moth increases the level of the parasitoid population at the edge of the outbreak. Then, by considering the phase plane for tussock moth and parasitoid, this shows that the tussock moth population level decreases at the edge of the outbreak. Finally, since the total number of moths in the outbreak region goes down, the area of the

outbreak decreases. We conclude that a reduction in the carrying capacity for the tussock moth leads to a reduction in both tussock moth density within the outbreak, and the size of the outbreak (Fig. 4).

Conclusions

The careful experimental, observational, and mathematical analysis of the system centered on bush lupines at Bodega Marine Reserve yields new insights into issues of pattern formation and population dynamics. Earlier work tended to focus separately on either the interaction between tussock moths and their parasitoids, or between bush lupines and the ghost moth herbivore. We have discussed here both our earlier insights, and the new kinds of ideas that can emerge from coupling these two pathways. The two modules of this foodweb are mirror images of one another. While the tussock moth disperses very slowly and its parasitoids disperse rapidly, the ghost moth disperses rapidly and the entomopathogenic nematode disperses very slowly. This disparity in relative dispersal rates, in combination with strong interactions, leads to many of the unusual dynamical properties of the system: the restricted spread of the tussock moth, the widespread deaths of lupine bushes due to ghost moths, and the inability of the nematode to control the ghost moth despite its potency as a predator.

External climatic forcing (Stenseth & Mysterud 2002) adds another element to the already high potential for large temporal fluctuations in this system. The recent work by Preisser and Strong (2004) demonstrates the strong effect exerted by ENSO events on the degree of protection given to lupine by the entomopathogenic nematode. This evidence suggests that ENSO years have a large effect on lupine survival and age structure. However, in non-ENSO years, the poor dispersal by the nematode in contrast to the mobility of the ghost moth means that large areas of lupine are not protected from the ghost moth caterpillars. Much of the resilience of the system is therefore likely to be due to the long-lived seed bank of the lupines (Maron & Simms 2001).

Our preliminary investigation of the higher-order interactions in this system yielded new

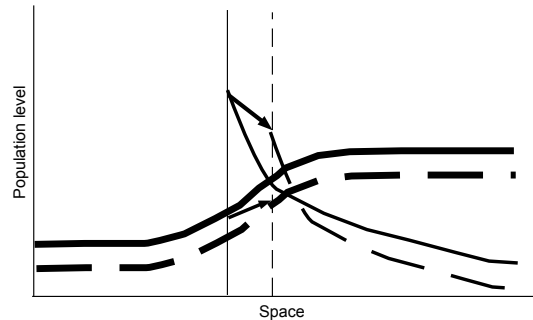


Fig. 4. Model results: effect of a reduction in the carrying capacity (bush lupine abundance) on tussock moth and parasitoid densities in continuous one-dimensional space. Thick line is tussock moth density, thin lines are parasitoid densities. Solid lines are before change in carrying capacity, dashed lines after carrying capacity is reduced. Note at the edge of the outbreak, parasitoid density goes up, tussock moth density goes down, and area of outbreak goes down.

and important predictions for the indirect effect of the ghost moth on the tussock moth, acting through changes in lupine density. The fluctuations in lupine density caused by the ghost moth are predicted to lead to the spatial retraction of the tussock moth outbreak, with an elevated relative level of parasitism at its edge. This contrasts with an alternative scenario in which the tussock moth population density declines everywhere but does not change its spatial location. Given the slow dispersal of the tussock moth, this effect could lead to significant time lags in the recovery of the tussock moth population following lupine population crashes.

Our model dealt only indirectly with temporal dynamics by contrasting static spatial patterns in two cases, one with higher and one with lower prey carrying capacity, and assumed density dependence in the exploiter. Thus our results leave many questions about temporal dynamics as yet unanswered. Would similar results be obtained if the stationary patterns resulted from an Allee effect (Owen & Lewis 2001)? What would the dynamics be if no stationary patterns in fact existed and only slowly traveling waves were present (as in the model used in Hastings *et al.* 1997 as shown by Owen and Lewis (2001))? It is also interesting to consider how the poorly dispersing tussock moth can track the dynamic changes in its resource base caused by the ghost

moth. Is there a maximum frequency of lupine population crashes with which the tussock moth can coexist? Does the tussock moth show temporal changes in abundance that is entrained by the ghost moth's dynamics? Is there an important dynamical role in this system for spatial refugia in which nematode densities and lupine survival are chronically high? All of these possibilities (and more) are suggested by the natural history of the system, yet are clearly beyond the level of complexity that is attainable here.

Our study illustrates that there is still much to be learned from the analysis and application of strategic models of spatial dynamics of interacting exploiters and victims. There may be few if any other systems with the exact properties and behaviors we have discussed here. However, many others may share some of the essential features, such as a moderately complex food web, strong trophic interactions, large differences in dispersal ability among interacting species, a spatially structured habitat, and powerful external perturbations. Our study shows how challenging it may be to understand and predict even the simplest spatial or temporal population behaviors when many or all of these elements are present. Nonetheless, our results based on a preliminary qualitative analysis of a qualitative model, are likely to be robust. For other systems with similar features, such as different time-scales and widely differencing dispersal scales among food web components, analyses such as ours may yield other novel insights.

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