

Defence against multiple enemies

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Abstract

Although very common under natural conditions, the consequences of multiple enemies (parasites, predators, herbivores, or even ‘chemical’ enemies like insecticides) on investment in defence has scarcely been investigated. In this paper, we present a simple model of the joint evolution of two defences targeted against two enemies. We illustrate how the respective level of each defence can be influenced by the presence of the two enemies. Furthermore, we investigate the influences of direct interference and synergy between defences. We show that, depending on certain conditions (costs, interference or synergy between defences), an increase in selection pressure by one enemy can have dramatic effects on defence against another enemy. It is generally admitted that increasing the encounter rate with a second natural enemy can decrease investment in defence against a first enemy, but our results indicate that it may sometimes favour resistance against the first enemy. Moreover, we illustrate that the global defence against one enemy can be lower when only this enemy is present: this has important implications for experimental measures of resistance, and for organisms that invade an area with less enemies or whose community of enemies is reduced. We discuss possible implications of the existence of multiple enemies for conservation biology, biological control and chemical control.

Introduction

Food webs in nature are generally complex, one species being attacked by many species of enemies (Hawkins *et al.*, 1997; Fellowes & Kraaijeveld, 1998; Sih *et al.*, 1998; Cox, 2001). Thus in natural systems, species potentially face diverse selective pressures from herbivores, predators and parasites. Most experimental and theoretical studies on trophic interactions have considered only species couples (one plant/one herbivore, one host/one parasite, or one host/one predator), and it is only recently that the importance and consequences of multiple enemies have been more thoroughly investigated (Sih *et al.*, 1998).

Experimental and theoretical studies show that population-dynamical interactions between enemies are often more complex than the simple addition of their effects in

isolation. For example, in biological control, the use of multiple enemies can be less efficient in controlling pest populations than the action of a single enemy (Mills, 2000). Depending on the specifics of the system, the addition of an enemy may enhance or reduce the risk of attack by another enemy (Sih *et al.*, 1998). More dramatically, the addition of an enemy can sometimes drive both enemies and their victim to extinction (Hochberg, 1996).

Interactions among many enemies may be influenced by direct or indirect competition, mediated by the effects of each enemy on the population dynamic of the host (Sih *et al.*, 1998). However, another potential factor involved in multiple enemy interactions is the reciprocal effect of enemies and their respective host-defences. For example, some defences are efficient against many enemies [for example, anti-microbial peptides act against many bacteria, or an increase in prey vigilance can act against many predators (Sih *et al.*, 1998)], while other defences may be efficient only against one enemy (e.g. secretion of specific antibodies, or modification of target molecules used by a pathogen to infect its host), or even

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make the victim more susceptible to other enemies (e.g. increased tegument thickness or other forms of physical protection can hinder escape mechanisms based on speed).

While defences are recognized to have an influence on enemy–victim interactions (Sih *et al.*, 1998), the reciprocal direction of causality has often been neglected. The level of investment in defence is usually studied only in relation to the selection pressure exerted by a single enemy and other factors like the history of the interaction between the enemy and its victim (Rydell *et al.*, 2000), or migration rates of enemy and victim (Lively & Jokela, 1996).

In this study, we develop a simple model to show how multiple enemies can be expected to influence the evolution of multiple defences. Two defences are considered, each primarily acting against one enemy. We search for the simultaneous evolutionary dynamics of both defences and for possible co-stable equilibria. We consider the action of several facets of the interaction, including the probabilities of attack by different enemies, the respective costs of relevant defences, and either direct interference or synergy between defences.

The model

We take an analytical approach to investigate how multiple defences are selected when a victim is confronted with two enemies. We search for optimal investment in both defences (i.e. investments that maximize the victim’s fitness) whilst considering victim fitness as a function of investment in defence *d* (effective only against enemy 1) and investment in defence *e* (effective only against enemy 2).

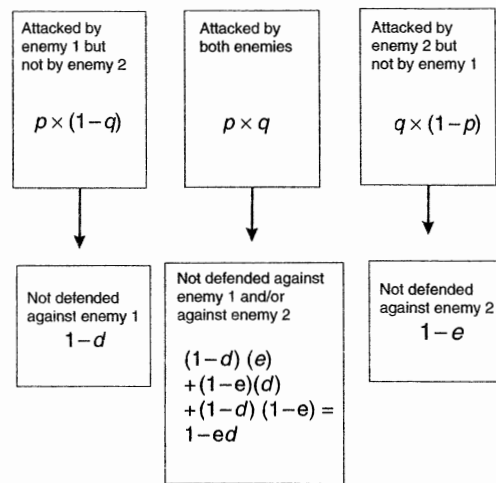
The victim’s fitness *w* is stated as:

$$w = b - p(1 - q)(1 - d) - pq(1 - de) - q(1 - p)(1 - e - cd^x - ke^y). \tag{1}$$

Here, baseline fitness, *b*, is the reproductive value of an undefended victim in the absence of enemies. The remaining negative terms reflect expected fitness losses endured by the victim as a result of successful enemy attack (second, third and fourth terms) and as a result of defence investment (fifth and sixth terms). Specifically, *p* and *q* are the encounter rates with each enemy (*p* for enemy 1 and *q* for enemy 2). Note that the probabilities of attack by both enemies are fixed, and independent of one another (thus the probability of being attacked by both is *pq*).

The event diagram in Fig. 1 illustrates the seven possible attack outcomes, and highlights the three scenarios where the enemy ‘wins’. Costs associated with a specific level of investment in defence *d* are determined by parameters *c* and *x*, whilst the cost of defence, *e*, is determined by *k* and *y*. Parameters *x* and *y* control the shape of the relationship between defences and their

Cases when there is a loss of fitness



Total :
 = $p(1 - q)(1 - d) + pq((1 - d)e + (1 - e)d + (1 - d)(1 - e)) + q(1 - p)(1 - e)$
 = $p(1 - q)(1 - d) + pq(1 - de) = q(1 - p)(1 - e)$

Fig. 1 Probability tree outlining the probabilities associated with each of the seven possible interactions. Where *p* is the encounter rates with enemy 1, measured as the risk of being attacked, *q* is the encounter rates with enemy 2, *d* is the level of defence against enemy 1, measured as the probability of resisting it or the reduction of its negative effects, and *e* is the level of defence against enemy 2.

costs. If *x* and *y* = 1, then costs increase linearly with defence. If *x* < 1 or *y* < 1, then cost increases decelerate with increasing defence. Finally, if *x* > 1 or *y* > 1, then costs accelerate with increasing levels of defence.

The victim’s strategy-set is thus defined by the two continuous variables, *d* and *e* (limited on the range 0–1). In the results below we present co-evolutionary optima for investment in *d* and *e*, as a function of enemy encounter rates (*p* and *q*) and costs of defence (*c*, *k*, *x*, *y*), and illustrate the broad inter-dependence in investment across the two defences. Furthermore, we adapt the above model (equation 1) to include the effects of direct interference between defences (i.e. inefficiency of defences when used simultaneously) or direct synergy between defences (i.e. efficiency gain when defences used simultaneously).

Results

In this model, it is important to note that the evolution of each defence is controlled by a balance between costs and the efficiency of defence in diminishing the impact of the enemy. This efficiency itself depends not only on the investment in defence and the encounter rate with the corresponding enemy but also on the encounter rate with the other enemy and investment in the other defence too: in cases when victims are attacked by both

enemies, they have to use both defences to resist – the efficient use of one defence alone may be useless.

The patterns we observed depended on the relationship between the efficacy of defences and their costs. With linearly increasing or decelerating costs (x and $y \leq 1$), maximal or minimal investments in defence favoured. In contrast, accelerating costs tend to create stable intermediary investments.

We focus on the case where the cost of investment in defence is accelerating. However, we start with a brief summary of the case where x and $y \leq 1$.

Linearly increasing costs and decelerating costs

Figure 2a,b illustrate the possible evolutionary outcomes for linearly increasing costs (x and $y = 1$) and decelerating costs (x and $y < 1$) (for calculations see the Appendix). For both linearly increasing costs and decelerating costs (i.e. high 'start-up' costs) there are four possible evolutionary outcomes: no investment in defence, investment only in one defence or in the other, or maximal investment in both defences. The presence or absence of these possible stable equilibria depends on the position of the isoclines. For example, in Fig. 2a the stable equilibria are (0,0) and (1,1), while in Fig. 2b the four outcomes – (0,0), (0,1), (1,0) and (1,1) – are possible. Importantly, the evolutionary outcome depends on the initial conditions of d and e . In particular, an initially low defence against one enemy can prevent investment in a separate form of defence acting against another enemy. This arises because when victims are attacked by both enemies and lack one form of defence, the other defence (against the other enemy) becomes useless.

Accelerating costs

For accelerating costs, an internal co-stable equilibrium can exist for investment in both defences (Fig. 2c). Accelerating costs favour intermediate levels of investment, as maximal levels of investment are too costly to be selected.

In Figure 3 this stable point for defence d is plotted against the encounter rates with enemies 1 and 2. Costs are assumed to be equal for both defences, so that the results are symmetrical for the second form of defence, e . The model illustrates qualitatively different behaviours as costs rise (summarized in Fig. 3).

At low costs (Fig. 3a), defensive investment is quickly maximized with increasing encounter rate with enemy 1, whereas the effect of enemy 2 is negligible. At intermediate costs (Fig. 3b), there is an interaction between the presence of enemy 2 and the investment in defence against enemy 1. This interaction is strongest at an intermediate level of encounter rate with enemy 2 and tends to reduce the investment against enemy 1. This can be explained by the interactive

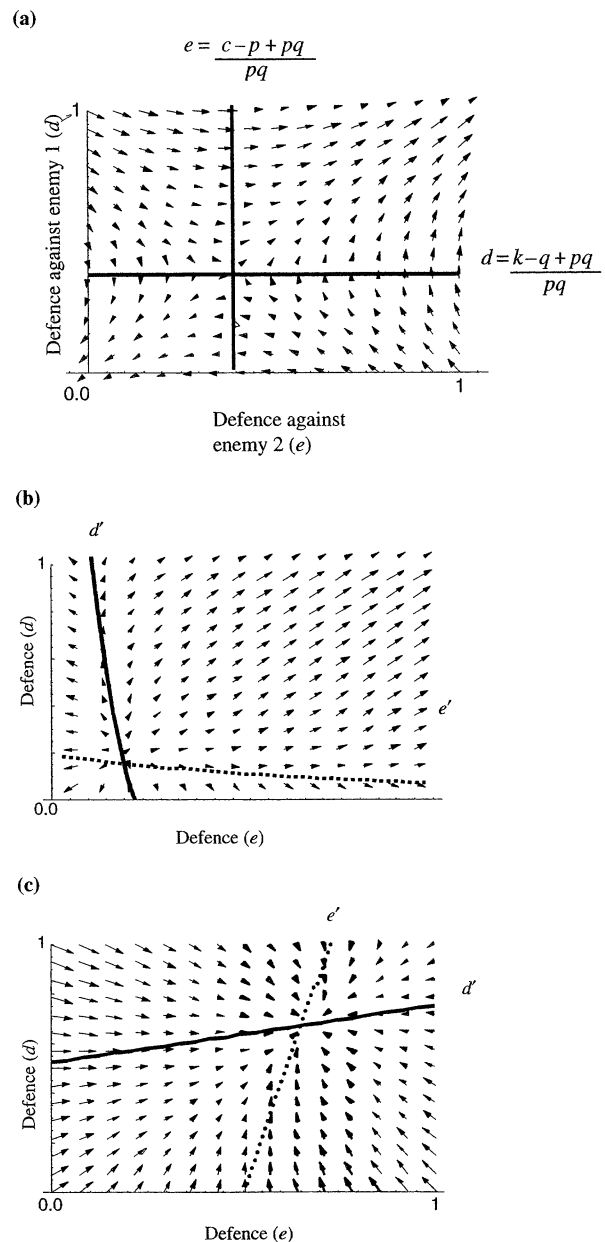


Fig. 2 (a) Phase diagram illustrating the simultaneous dynamics of the two defensive traits when the costs are linearly increasing ($x = y = 1$). The horizontal line is the isocline for $dw/dd = 0$, separating regions in which d increases or decreases. Similarly the vertical line is the isocline for $dw/de = 0$. Parameter values are: $c = k = 0.3$, $p = q = 0.4$. (b, c) Phase diagram illustrating the joint dynamics of the two defensive traits, when there is a decelerating increase in cost (b: $x = y = 0.5$) and when there is an accelerating increase in cost (c: $x = y = 2$). The solid line is the isocline for $dw/dd = 0$ [fitness minimum for (a), fitness maximum for (b)], the dotted line is the isocline for $dw/de = 0$. For accelerating increase in cost, the intersection between the isoclines is a co-stable equilibrium point. For both figures, parameter values are: $c = k = 0.2$, $p = q = 0.3$.

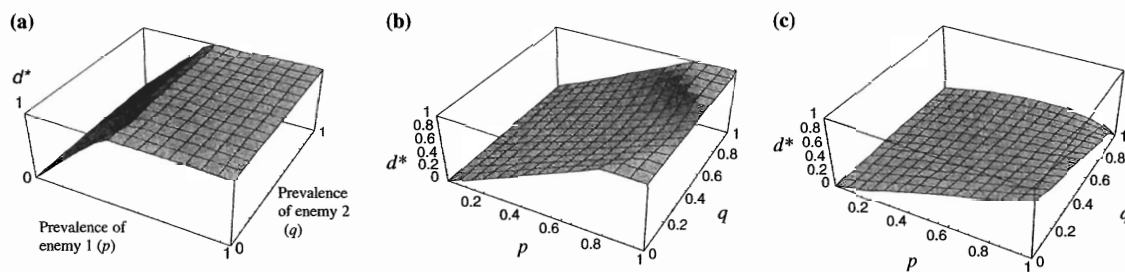


Fig. 3 Optimal investment in defence d (against enemy 1) plotted against encounter rates with enemies 1 and 2, for increasing costs of defence c and k . As $c = k$, plots of optimal investment in the other defence (e) are symmetrical (investment in e is equal to investment in d for inverted values of p and q). Parameter values are: (a) $c = k = 0.2$, (b) $c = k = 0.4$, (c) $c = k = 0.6$.

effect of enemy encounter rates and the joint evolution of defences. An increase of probability of attack by enemy 2 increases cases when victims are attacked by both enemies. If defence against enemy 2 is low or moderate, the advantage of increasing defence 1 is reduced (as defence against enemy 1 is useless if the victim is not defended against enemy 2). But an increase in encounter rate with enemy 2 increases selection pressure on defence 2 too, modulating this effect. Under conditions of moderate cost, this modulation is most clear, and more effective at high encounter rate with enemy 2 (as defence e is then high enough to annul the inhibitory effect on d of defencelessness against enemy 2).

Finally, at high cost (Fig. 3c), the presence of enemy 2 lowers the investment in the defence against enemy 1, leading to an abandonment of defence when both encounter rates are high. This parallels the results of van Baalen (1998) and Sasaki & Godfray (1999) on defensive abandonment in the face of increasing challenge with a single enemy. The mechanism of interaction of defences is the same as for medium cost (Fig. 3b), except that at high probabilities of attack by both enemies, the cost of defence is too high to invest simultaneously in both defences, leading to an abandonment of defence.

Mechanistic interference among defences

In the above model, we supposed that there is no direct interaction between defences against enemies. However, in some cases one might expect that the use of one defence has a negative effect on the efficiency of another. For example, Rigby & Jokela (2000) illustrated how the anti-predator defence of a snail increases its susceptibility to pathogens. Behavioural defences such as hiding or camouflage can have interfering effects too, for example camouflage against one enemy may increase the risk of being killed by another (Pitt, 1999). Some physiological reactions against enemies inhibit the expression of other antagonistic pathways (Maleck & Dietrich, 1999), and thus may interfere with levels of resistance to other enemies.

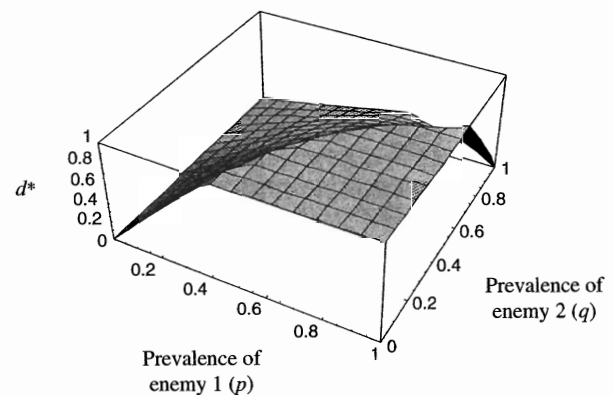


Fig. 4 Defensive investment given interference between defences. Optimal investment in defence against enemy 1 (d) plotted against encounter rates with enemies 1 and 2, when there is a negative interaction between defences ($i = 0.8$). The results for investment in defence against enemy 2 (e) are symmetrical. Cost values are: $c = k = 0.2$.

To examine the effects of such interference between defences, we modified the first model (equation 1) to introduce a decrease in defence efficiency when attacked by both enemies.

$$W = b - p(1 - q)(1 - d) - pq[1 - de(1 - i)] - q(1 - p)(1 - e) - cd^x - ke^y \quad (2)$$

Here, parameter i determines the force of the interference. Where i ranges from 0 to 1: if $i = 1$ it is impossible to defend against both enemies, even if there is maximal investment in both defences. If $i = 0$ the defences act independently, and we recover equation 1. Note that the effect of i acts symmetrically on both defences.

Not surprisingly, interference between defences increases investment thresholds when costs are linear or decelerating (x and $y \leq 1$), and lowers the investment in defence for accelerating costs. These effects of interference increase with enemy encounter rates. For example, in Fig. 4 mechanistic interference can have a drastic

effect on defensive investment (compared with Fig. 3a): increasing the encounter with a second enemy ensures a diminishing investment in defence against the first.

Defensive synergy: engaging d induces resistance against enemy 2

Here we introduce the idea of a 'red alert' defence, a defence that once provoked will act not only against its instigator but also against a second enemy as well. Note that this is not a constitutively generalist defence: it needs to be activated by an attack of one enemy to be efficient against the other, thus becoming a generalist defence. For example, human cowpox typically elicits an effective immune response, which in addition to giving protection against further cowpox infection, offers protection against smallpox. In contrast, direct challenge with smallpox alone elicits a far weaker host defensive response (Jenner, 1801). Similarly, some plants challenged by herbivores are more resistant to fungal infections than un-challenged plants (Paul *et al.*, 2000).

To incorporate defensive synergy, we modify the initial model (equation 1) to allow defence d – once initiated by enemy 1 – to act against enemy 2 (equation 3). Here, the parameter s determines the level of protection delivered by defence d against enemy 2, and s ranges from 0 to 1: if $s = 1$, defence d protects totally against enemy 2. If $s = 0$, there is no effect of defence d against enemy 2, and we recover equation 1.

$$W = b - p(1 - q)(1 - d) - pq[1 - de - d(1 - e)s] - q(1 - p)(1 - e) - cd^x - ke^y \quad (3)$$

This model does not consider the effect of attack order. It assumes that enemy 1 always attacks simultaneously with or before enemy 2. However, introducing an order effect does not qualitatively change the results (not shown).

Allowing one defence (d) to have an action against both enemies, ensures that it becomes more independent from the encounter rate with enemy 2 (cf. Fig. 5a,b with Fig. 3b,c) as the victim is defended against it via d . For the other defence (e), the synergistic role of d ensures a drastic drop of defence e with increasing encounter rates with both enemies (cf. Fig. 6b with Fig. 6a). But at high

costs (cf. Fig. 6d with Fig. 6c), this effect is slight: without synergistic resistance, the level of resistance was already collapsing due to prohibitive costs. For high costs and high encounter rates, there is even a positive effect of synergy on the level of resistance e , due to the cost-saving effect of synergistic defence d .

Defensive synergy: engaging one defence induces resistance against both enemies

Here we examine a symmetric version of the previous model (equation 3), to include a reciprocal synergistic effect between the two defences. The two defences can either be interpreted as separate defensive mechanisms (each offering a more-or-less generalized protection once induced), or as a single generalist defence, induced through two separate pathways (corresponding to d and e).

For example, plant defences (or a single generalized defence) elicited by different enemies may vary in their efficiency against a range of enemies subsequently encountered by the plant (Agrawal & Karban, 1999). To incorporate a simultaneous synergy in defensive investment, we modify equation 1 as follows:

$$w = b - p(1 - q)(1 - d) - pq[1 - de - d(1 - e)a] - q(1 - p)(1 - e) - cd^x - ke^y \quad (4)$$

Here a controls the degree of synergy in victim defence. If $a = 1$, then being attacked by one enemy entails a defence equally efficient against both (the effect is the same as in the former section but with symmetrical effect). If $a = 0$, then the defences act independently and we recover equation 1.

The main consequence of a symmetric synergy in defence is a decrease in defensive expenditure when costs are low and encounter rates with enemies are high (cf. Fig. 7a with Fig. 3a): to obtain the same level of defence, victims need to invest less because both defences act against both enemies (i.e. victims gain more 'value for money' in their investments). However, when both costs and encounter rates are high, synergistic interactions permit a higher investment in both defences: the cost of being attacked by both enemies and not defended against one is limited by synergistic defence (cf. Fig. 7b with Fig. 3c).

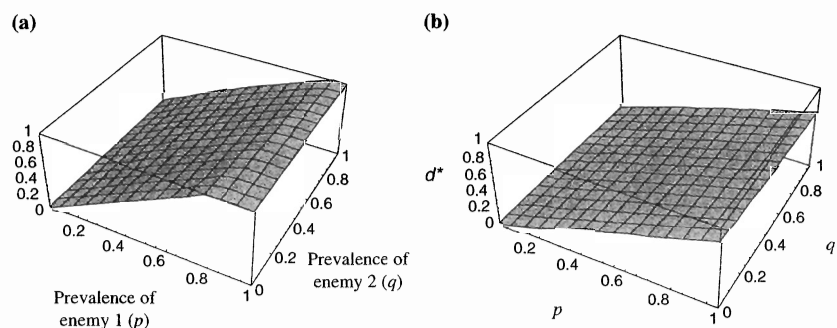


Fig. 5 Defensive investment in defence against enemy 1 (d) given synergistic resistance. Parameter values are: $s = 0.8$, Fig. 6a: $c = k = 0.4$; Fig. 6b: $c = k = 0.6$.

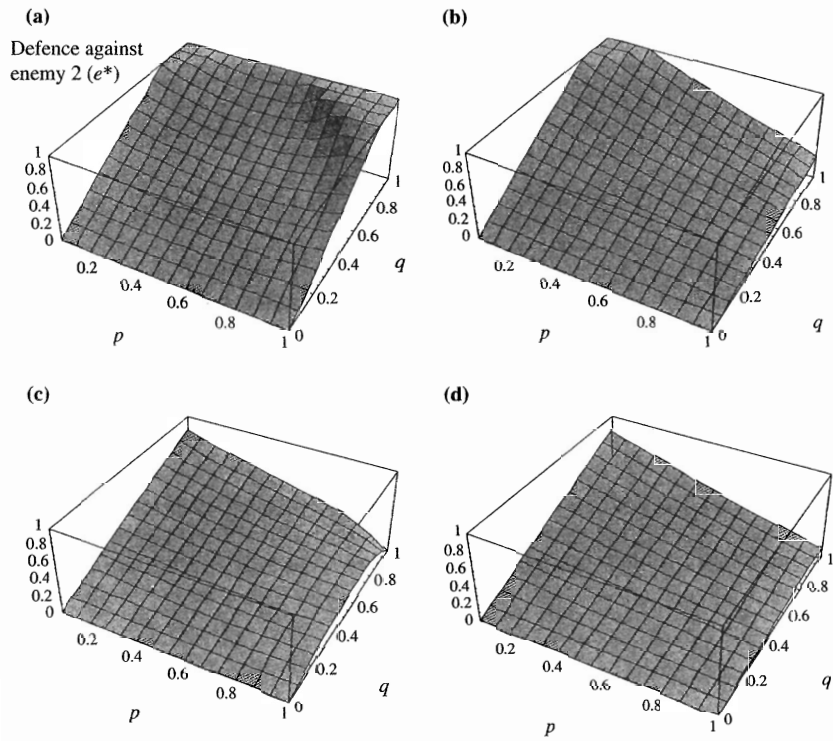


Fig. 6 Optimal investment in defence against enemy 2 (e) plotted against encounter rates with enemies 1 and 2. (b) and (d) present results with synergistic effects ($s = 0.8$), while (a) and (c) are plots of optimal investment in defence e when there is no synergy ($a = 0$). Cost values for (a) and (b) are: $c = k = 0.4$, and for (c) and (d): $c = k = 0.6$.

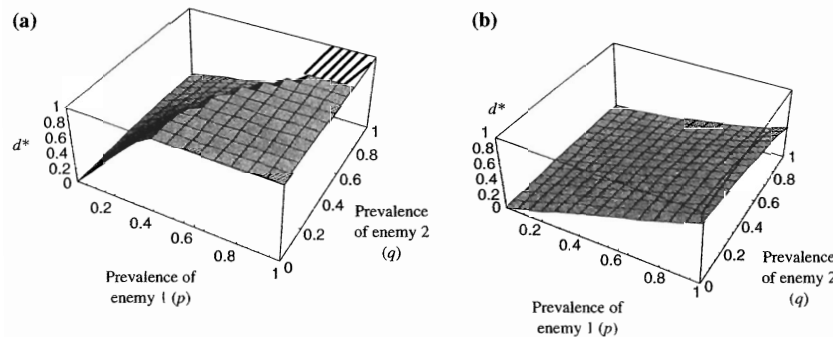


Fig. 7 Optimal investment in defence against enemy 1 (d) plotted against encounter rates with enemies 1 and 2, when there is mutual cross resistance ($a = 0.8$). The results for investment in defence against enemy 2 (e) are symmetrical. The dashed area of Fig. 7a corresponds to an area where there is two possible evolutionary outcomes (cf. Fig. 8). Cost values for (a) are: $c = k = 0.2$, and for (b): $c = k = 0.6$.

Given sufficiently high synergy and high encounter rates with both enemies, there are two possible evolutionary outcomes (Fig. 8): a maximal investment in one defence, and an intermediate investment in the other, or *vice versa*. Which defence is maximized depends on initial conditions, the highest defence winning the investment 'competition', offering a generalist defence (almost guaranteed to be induced for sufficiently high encounter rates) against both enemies.

It is important to note that this synergy of defences tends to decouple the defence that is active against one enemy from the cues that induce this defence. The important consequence is that a change in encounter rate with one enemy will have consequences on the level of defence selected against the other enemy: an

increase in encounter rate with one enemy would increase the induction of defence active against the other, while a decrease of encounter rate with one enemy would induce a transient decrease in the total defence against the other, before the evolution of a higher specific defence. A study of the level of defence against one enemy in the absence of others would therefore not be representative of situations that could occur in natural systems, where defences are induced by multiple enemies: defence would seem lower than it actually is. Paradoxically, a species that has evolved its defences in an environment with multiple enemies could be more susceptible to enemy attack if it is placed in a new environment where fewer enemies are present.

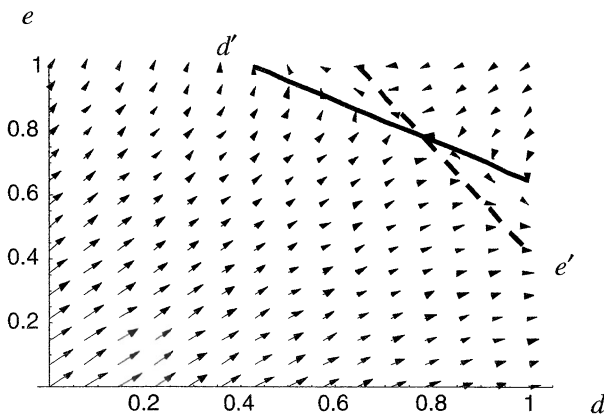


Fig. 8 Phase diagram illustrating the joint dynamics of the two defensive traits in the dashed area of (a). The plain line is the isocline for $dw/dd = 0$ (fitness maximum), the dotted line is the isocline for $dw/de = 0$. Parameter values are: $p = q = 0.9$; $c = k = 0.2$; $a = 0.8$.

Discussion

Our results highlight the importance of evolutionary change in multiple-enemy interactions. For instance, we demonstrate that even in the absence of mechanistic interactions between two defences, the level of investment in one defence can determine whether investment in a second defence is favoured. The presence of a second enemy can favour the evolution of either higher or lower defence against the first enemy (and *vice versa*), with the direction of evolutionary change being dependent on enemy encounter rates, defensive costs and possible mechanistic interactions between the defences.

In our analysis we assumed three possible relationships between defence and its cost: defence increasingly less costly, defence in which cost is linearly increasing, and defence with accelerating cost. We mainly focussed on the case with accelerating costs. It is well established that the shape of this relationship can be important to the evolutionary outcome of trophic interactions (Franck, 1991). Although it is difficult to quantify costs (Boots & Haraguchi, 1999; Coustau *et al.*, 2000), one can infer the basic form of the relationship between cost and level of defence from knowledge about the mechanism of defence and the types of costs involved (Boots & Haraguchi, 1999). For example, defences based on cuticle or shell thickness should have costs associated with the volume of cuticle/shell produced. As volume increases at a faster rate with thickness than thickness itself, one should expect such costs to accelerate with level of defence. In contrast, some defences that need a minimal investment (a 'start-up cost') to be efficient (cf. morphological defences like spines or the constitutive part of the immune system) would have a cost asymptotically increasing with efficiency of defence. But it seems unlikely that the increase of costs with resistance should

decrease indefinitely: a more realistic trade-off curve would be sigmoidal, cost being increasingly less costly for low levels of defence (the mounting of the defence), but increasingly more costly for sufficiently large levels of defence (Boots & Haraguchi, 1999). The results of Boots and Haraguchi suggest that the concave part of the sigmoidal function dominates evolutionary dynamics, but further investigation is needed to confirm this finding for a wider range of models.

For sufficiently high defensive costs and high enemy encounter rates we found that investment in defence may be entirely abandoned (particularly given mechanistic interference, Fig. 4). This could have implications for the classical biological control of arthropod pests, where one or more exotic natural enemies are released for the control of an invading pest. Combining the use of multiple biological agents may prevent the evolution of high levels of resistance, provided there is no synergistic resistance (Figs 2 and 3). Given synergistic resistance (Figs 5–7), a multiple-enemy control strategy will be less efficient. A parallel can be made between resistance to biological and chemical 'enemies': with the rapid increase of insecticide (Georghiou, 1986) and antibiotic resistance (Bonhoeffer *et al.*, 1997), the question of the optimal use of chemical controls is increasingly investigated. The concomitant use of many chemicals has been advised to slow the increase of resistance (Bonhoeffer *et al.*, 1997; Hoy, 1998; Roush, 1998; White, 1999). Our model can easily be modified to study the effect of a strategy of double-chemical control on equilibrium levels of resistance, by modifying the current assumption of independence between attack probabilities p and q .

Throughout our analyses, we assume that the probabilities of attack by both enemies are independent and fixed, and we exclude coevolutionary interactions between the victim and its enemies. Hence, this model is more realistic for interactions with generalist enemies whereby feedbacks between encounter rate with the enemy and investment in defence are less likely to occur, or populations of enemies where migration between populations can diminish the population-dynamical effect of local resistance, or finally for chemical 'enemies', incapable of evolutionary or population-dynamical response. Examining the consequences of modifications to these assumptions (e.g. nonindependence among enemy attack, population-dynamical and evolutionary responses in enemies) represents promising lines of future theoretical research.

From an empirical perspective, more research is needed on the interaction between multiple enemies and defence. Most studies on multiple enemies do not consider evolutionary perspectives, focusing rather on the population dynamics of multiple-enemy systems (Bonsall & Hassel, 1999; Shimada, 1999) or the mechanisms of defences against multiple enemies (Maleck & Dietrich, 1999; Pitt, 1999). Future studies comparing defensive evolution under selective pressures from one

or many enemies, or less directly studies on the level of defence across species in communities differing in the number of natural enemies should help to better understand defensive evolution in a multiple enemy context.

Acknowledgments

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Appendix

Model without mechanistic interactions between defences

To study the dynamics of the model, we search for the solutions to the equations $dw/dd = 0$ and $dw/de = 0$, which define the isoclines where defences d and e are minimal/maximal.

The general solutions are:

$$d' = \left[\frac{cx}{p(1-p+eq)} \right]^{\frac{1}{1-\gamma}}$$

$$e' = \left[\frac{ky}{q(1-p+dp)} \right]^{\frac{1}{1-\gamma}}$$

For accelerating costs [$(x,y) = 2$], the intersection(s) of isoclines (stable point of equilibrium) are the solution(s) to the equations:

$$d^* = \left[\frac{cx}{p(1-q+e^*q)} \right]^{\frac{1}{1-\gamma}} \quad \text{and} \quad e^* = \left[\frac{ky}{q(1-p+d^*p)} \right]^{\frac{1}{1-\gamma}}$$

Rearranging terms, we find:

$$d^* = \frac{p(-2k + 2kq - q^2 + pq^2)}{Ack - p^2q^2}$$

$$e^* = \frac{q(-2c + 2cq - p^2 + pq^2)}{4ck - p^2q^2}.$$

Model with interference between defences

The isoclines for d and e are defined by the equations:

$$d' = \left[\frac{cx}{p(1 - q + eq - ieq)} \right]^{\frac{1}{1-x}},$$

$$e' = \left[\frac{ky}{q(1 - p + dp - idp)} \right]^{\frac{1}{1-y}}.$$

The stable equilibrium when x and $y = 2$ is found as:

$$d^* = \frac{p(-2k + 2kq - q^2 + pq^2 + iq^2 - ipq)}{4ck - p^2q^2 + 2ip^2q^2 - i^2p^2q^2},$$

$$e^* = \frac{q(-2c + 2cp - p^2 + qp^2 + ip^2 - ipq^2)}{4ck - p^2q^2 + 2ip^2q^2 - i^2p^2q^2}.$$

Model with synergy between defences

The isoclines for defences d and e are defined by:

$$d' = \left[\frac{cx}{p(1 - q + eq - sq + seq)} \right]^{\frac{1}{1-x}},$$

$$e' = \left[\frac{ky}{q(1 - p + dp - sep)} \right]^{\frac{1}{1-y}}.$$

The (stable point) equilibrium when $x = y = 2$ is:

$$d^* = \frac{p(-2k + 2kq - q^2 + pq^2 - 2akq + aq^2 - apq^2)}{4ck - p^2q^2 + 2ap^2q^2 - a^2p^2q^2},$$

$$e^* = \frac{q(-2c + 2cp - p^2 + pq^2 + ap^2 - 2ap^2q + a^2p^2q^2)}{4ck - p^2q^2 + 2ap^2q^2 - a^2p^2q^2}.$$

Model with mutually crossed defences

The isoclines for defences d and e are defined by equations:

$$d' = \left[\frac{cx}{p(1 - q + eq + aq - 2aeq)} \right]^{\frac{1}{1-x}},$$

$$e' = \left[\frac{ky}{p(1 - p + dp + ap - 2adp)} \right]^{\frac{1}{1-y}}.$$

The (stable point) equilibrium for $x = y = 2$ is:

$$d^* = \frac{p(-2k + 2kq - q^2 + pq^2 + 2akq - 2aq^2 + 3apq^2 - 2a^2pq^2)}{4ck - p^2q^2 + 4ap^2q^2 - 4a^2p^2q^2},$$

$$e^* = \frac{q(-2c + 2cp - p^2 + qp^2 + 2acp - 2ap^2 + 3apq^2 - 2a^2qp^2)}{4ck - p^2q^2 + 4ap^2q^2 - 4a^2p^2q^2}.$$