Forum

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Error management in plant allocation to herbivore defense

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Herbivores can greatly reduce plant fitness. Error management theory (EMT) predicts the evolution of adaptive plant defensive strategies that err towards making less-costly errors so as to avoid making rare, costly errors. EMT provides a common framework for understanding observed levels of variation in plant defense among and within species.

Adaptive errors as a solution to uncertainty regarding herbivore attack

Plants face the dilemma of uncertainty of attack by herbivores that seek to consume their tissue. Despite a large body of work on plant defense [1–3], a large amount of variation in defense allocation remains unexplained: plants rarely perfectly match investment in defense to the cost of attack. Error management theory (EMT) [4] formalizes how evolution by natural selection is expected to favor organisms that consistently make errors in defense allocation; such errors are adaptive if they reduce the likelihood of making a more costly type of error (Box 1, Figure 1). In this paper, we describe how EMT can explain variation in defense allocation, help inform plant defense theory, and provide testable hypotheses regarding the allocation of defense and how plants use information.

A primer of plant defense and error management

Plants defend themselves via traits that reduce the amount of herbivore damage (resistance [3]), reduce the effect of herbivory on fitness (tolerance [3]), or both. In this paper, we use 'defense' to describe both resistance and tolerance. We focus primarily on defenses that are plastic (i.e., induced defenses [1], Box 2), where some cue (e.g., chewing damage from a herbivore) causes a change in allocation to resistance [1] or tolerance (reviewed in [5]).

Because of the uncertainty of herbivore attack, plants necessarily make two different types of errors in allocation to defense (Box 1). A plant makes the error of unnecessary defense if it invests in defense but herbivores do not attack. Alternatively, a plant might err by failing to allocate to needed defense. Importantly, the costs (or benefits) of these two types of errors are often very different (e.g., the cost of an undefended attack might be severe compared with the cost of unnecessary defense). The challenge of optimization amidst uncertain outcomes with asymmetrical costs and benefits is not unique to plant–herbivore interactions. Similar challenges are described in engineering, human psychology, animal communication, and predator–prey interactions, for example, the 'ecology of fear' (reviewed in [4,6]). EMT, developed from signal detection theory, provides a general theoretical framework applicable to these diverse situations [4,6]; EMT formalizes the notion that, when errors are unavoidable, benefit is maximized by biasing allocation (or choice) to minimize the likelihood of the more expensive type of error (at the cost of increasing the likelihood of the less-expensive type of error). For example, smoke detectors are engineered with a bias towards false-positive errors (e.g., going off when you burn toast) to avoid making the more costly false-negative error of failing to detect an actual fire. EMT focuses on evolutionary consequences of error management, as natural selection is expected to favor organisms that bias allocation towards making the least-costly error, which reduces the likelihood of making the more-costly error (Box 1).

EMT informs and strengthens the study of plant defense

Because it focuses on fitness in evolutionary time, a primary lesson from EMT is that allocation to defense is shaped by errors with unequal costs and benefits that are many generations removed from present-day defenses. The focus of EMT on evolutionary timescales, probabilistic attack, and different error costs can help strengthen plant defense theories. These theories often focus on allocation to defense over short timescales [2,3] and lack the explicit mathematical framework of EMT for predicting when defense should be initiated (Box 1). Because EMT and existing plant defense theories both include cost–benefit considerations [2,3], EMT can be incorporated into existing plant defense theory. Doing so can help unify plant defense

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Box 1. Error management for plants under the risk of consumption

When information can be used to predict consumption risk, organisms should allocate resources to defense only when available information indicates that the fitness benefits of action outweigh the costs of inaction; this general problem is developed within signal detection theory [6]. This requires that organisms use a decision threshold where allocation to defense is triggered [6]. For example, consider a plant that detects some concentration of volatile cues from a wounded neighbor; in this case, the decision threshold is the concentration of the cue where the focal plant would induce defense. The value of the decision threshold determines the likelihood of successful defense and the potential for two different types of errors: allocating to unnecessary defense (i.e., a false alarm or false positive) or failing to allocate to necessary defense (i.e., a false negative). A low decision threshold means that the focal plant would induce defense in response to a low concentration of volatile cue. Such a strategy has the benefit of reducing false-negative errors (i.e., the plant is unlikely to experience undefended attack), but at the cost of higher false-positive error rates (i.e., the plant is more likely to pay the cost of unnecessary defense). By contrast, a high decision threshold means that the plant might not defend in response to high concentrations of volatile cues. This strategy trades fewer false alarms for a higher likelihood of failing to defend when necessary (i.e., a false-negative error).

EMT emphasizes that selection can produce organisms that make adaptive errors, that is, that use a decision threshold that maximizes the fitness benefit to the organism (i.e., EMT is analogous to expected utility theory but cast in evolutionary time). Optimal error management is a function of the probability that the signal represents the occurrence of a herbivore, $P(h)$, the probability that the signal is simply noise, $P(n)$, and the relative value of the four different possible outcomes: True Positive (TP; correct defense), False Positive (FP; unnecessary defense), True Negative (TN; correct lack of defense), and False Negative (FN; undefended attack). Given those parameters, the optimal decision threshold (D) [6] is:

$$D \geq \frac{P(n)}{P(h)} \times \frac{(TN + FP)}{(TP + FN)} \qquad [I]$$

In the example figure (Figure I), the decision threshold is 1, and the heights of the two distributions are identical. As D increases, the threshold becomes more stringent, and allocation to defense occurs at greater amounts of the cue. Note that when the errors have equal costs, the optimal decision threshold is a function of the background probability of attack (i.e., the first term in the equation) and the relative benefits of correct outcomes (i.e., TN or TP).

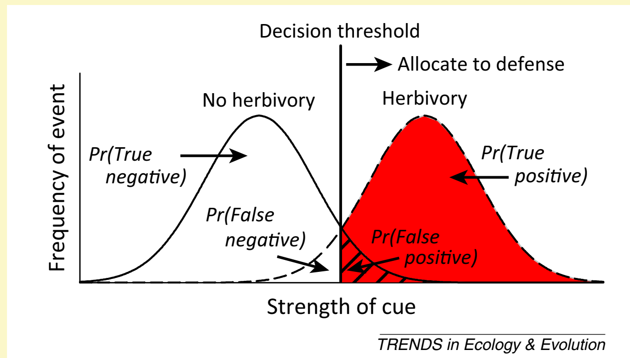

Figure I. When information (e.g., a cue from the environment) can be used to reduce uncertainty regarding attack, false-negative and false-positive errors in defense allocation are important components determining the optimal level of a cue where defense should be initiated. This decision threshold (D) is expressed as the ratio of the probability density of the distribution for herbivory divided by the density of the distribution for no herbivory.

theory (sometimes referred to as a quagmire [2]), inform current debates (Box 2), reconcile equivocal tests of existing theories, and provide new testable predictions.

A framework for general predictions about plant defense in light of EMT

EMT allows specific predictions with regard to when plants should initiate defense once costs and benefits of errors and the probability of attack are quantified (Box 1). Importantly, precise estimation of these parameters is not strictly required to use EMT to explore plant defense, as EMT makes testable qualitative predictions; similar to optimal foraging theory in animal behavior [7], qualitative predictions of EMT for plant defense might stimulate significant discovery.

Costs and components of plant error management

Predictions regarding plant allocation to defense can be generated by considering costs of consumption and defense among plant species or among plants of the same species in different ecological situations (Figure 1). Because seedlings are less likely to survive even modest amounts of partial consumption, for example, EMT predicts that they should err towards unnecessary constitutive defense or require relatively little information to trigger induction of defense (i.e., a bias away from false-negative errors). At the other extreme, trees and large adult plants might weather low-to-moderate levels of herbivory with little impact on fitness. While a dichotomous classification of seedlings versus adult plants (or even plants versus animal prey) is superficially appealing, the critical distinction is the rate of fitness loss with consumption rather than some other classification. Although we focus on plant–herbivore interactions, this logic also extends to other heterotrophic interactions: the decision threshold (Box 1) for organisms defending against virulent pathogens should be lower than for less virulent parasites or pathogens and the decision threshold for prey defending against lethal predators should be lower than that against predators whose attacks rarely reduce fitness.

Error management and the frontier of plant information use

EMT highlights how diverse cues of risk used by plants [8–10] might be compared and manipulated to understand the evolution of plant defense allocation and information use. EMT predicts that the level of cue needed to trigger defense will depend on the evolutionary history of the plant (e.g., how catastrophic the attack will be and how often it occurs) and the ecological situation of the plant (e.g., plant size, competitive environment; Figure 1). Importantly, these EMT predictions are amenable to experimental testing because information (e.g., general cues such as jasmonate or trichome damage, or specific cues such as mucus application [8,10]) and ecological situation (e.g., resource limitation) can be manipulated for species that differ in their evolutionary history.

Evolutionary context should affect allocation. Plants with an evolutionary history of costly attack should exhibit a consistent bias towards unnecessary defense compared

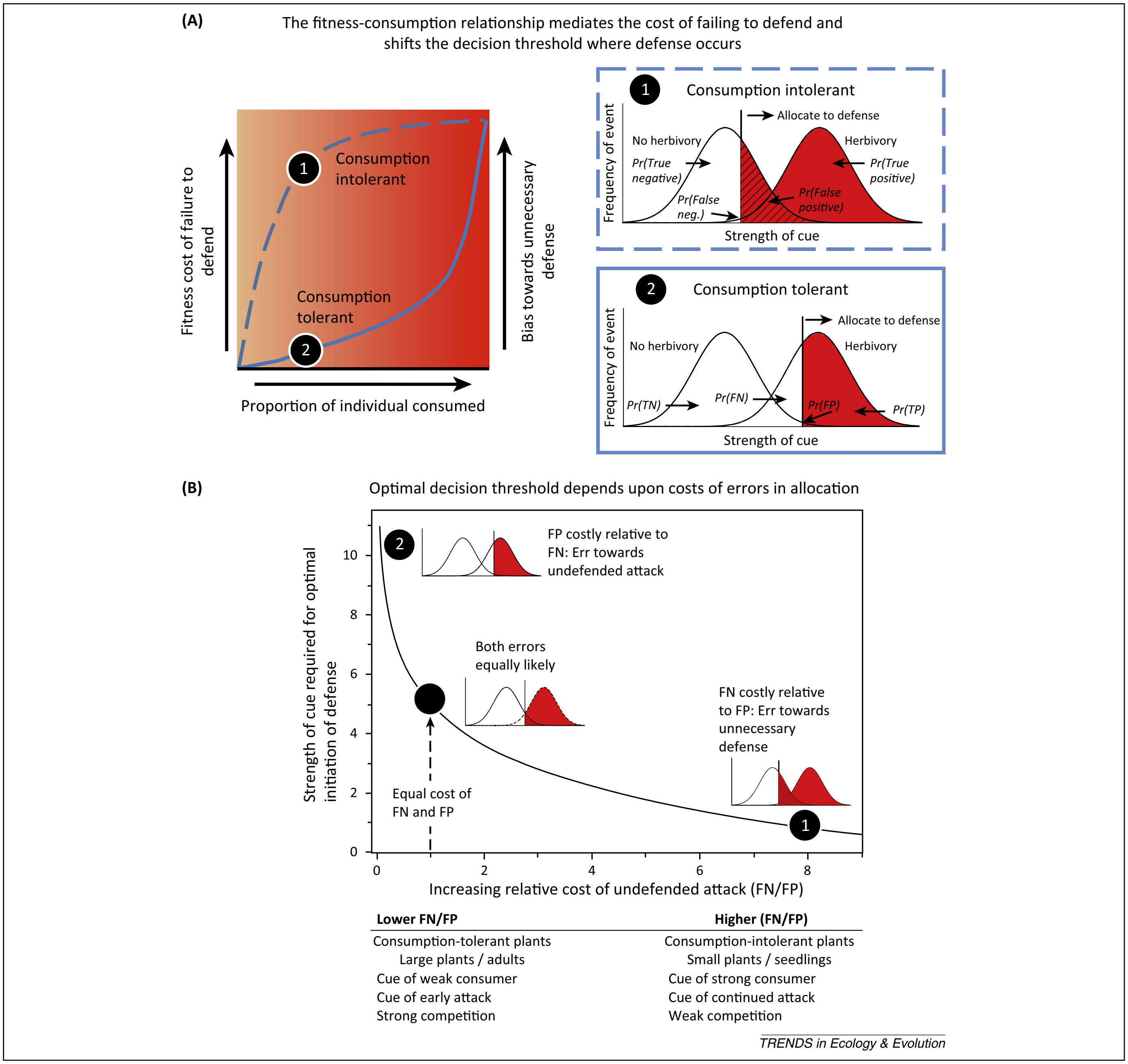

Figure 1. Error management theory and plant defense. **(A)** Once consumption begins, organisms will experience a loss of fitness; the rate of this loss is likely to vary among organisms. This simple model classifies organisms into two categories: those that incur heavy losses of fitness with modest amounts of consumption (consumption-intolerant organisms, **1**) and those that incur slower losses of fitness with increasing consumption (consumption-tolerant organisms, **2**). The relationship between fitness loss and consumption is important because it describes the relative costs of failing to defend, that is, the costs of a false-negative error. For example, for consumption-intolerant organisms (e.g., seedlings) the cost of failure to defend becomes large as soon as there is any appreciable consumption. For typical mature plants (or any organism that can withstand partial consumption), the cost of failure to defend becomes appreciable only late in the interaction, after considerable consumption has occurred. Because the cost of failing to defend is likely very high for consumption-intolerant organisms **(1)** optimal error management predicts a high probability of false-positive errors (unnecessary defense) and a low probability of false-negative errors (failing to defend). For organisms that can tolerate some consumption **(2)**, the cost of unnecessary defense is likely higher relative to the cost of failing to defend, and optimal error management predicts a decision threshold that minimizes false-positive errors at the cost of increasing the likelihood of false-negative errors. **(B)** Optimal error management, represented as the optimal level of the cue required to initiate defense as a function of the relative cost of an undefended attack (i.e., the cost of FN/the cost of FP). When costs of unnecessary defense are high relative to costs of undefended attacks, the optimal approach is to allocate to defense in a way that minimizes the likelihood of a costly false-positive error. When costs of undefended attack are relatively high, however, allocation to defense should instead occur at relatively small amounts of the cue, reducing the likelihood of a costly false-negative error (lower right corner). The relative effect of error management is evident by comparing optimal cue thresholds with the case where errors have equivalent costs. Values generated with Equation I in Box 1, assuming $P(h) = P(n) = 0.5$, TN = TP = 0, FP = 1, and FN ranging from 0.1 to 10. To provide units for the cue level, we assume Gaussian distributions for the noise distribution (mean = 4, SD = 2) and herbivore distribution (mean = 6, SD = 2).

with plants with a history of less costly attack. In the context of induced defense, EMT predicts that the amount of information needed to trigger allocation of resources to defense should differ predictably among species (Figure 1). For example, consider two plant species that pay the same fitness costs for unnecessary defense but experience different fitness costs of an undefended attack (Figure 1). EMT predicts that the species that experiences greater fitness costs of undefended attack will induce defenses in response to lower amounts of risk cue (e.g., volatiles from an

Box 2. EMT can help clarify current topics in plant defense

The efficacy of induced defenses, especially in light of possible costs to maintaining the capacity for induction, hinges critically on the ability to use cues to predict the risk and/or cost of an attack. Given that induced defenses have been found to be nearly ubiquitous and often tailored to particular traits of specific attackers [1,12], an important question is the degree to which plants utilize constitutive defenses that are always expressed versus induced defenses that are expressed in response to a cue.

Error management can inform the relative utility of both of these strategies – induced defenses minimize costs of false-positive errors while constitutive defenses provide a means to minimize costs of false-negative errors, especially when information is not available for predicting the initial attack (a situation that favors evolution of constitutive defenses, which are still expected to be molded by EMT). After an initial attack, plants might also be less likely to make a false-positive error (i.e., plants will rarely make the false-positive error of mistaking consumption for a false alarm once consumption is underway). The low cost of false-negative errors for many plants and lower likelihood of false-positive errors following initial attack should select for organisms capable of mounting rapid induced defenses and using past experience to inform future defense allocation. This perspective is consistent with defensive priming in plants, where previous exposure to risk cues facilitates rapid induction following an attack [5,12].

attacked neighbor). If consumers differ in their fitness costs to plants, EMT predicts that plants will respond to lower levels of a cue from a highly destructive herbivore (i.e., a herbivore with a high cost of undefended attack) compared with the cue from a herbivore that has small effects on plant fitness. EMT also predicts that plants might make maladaptive errors of allocation when faced with novel herbivore cues, that is, evolutionary traps [11]. For example, plants might fail to allocate to defense in response to an exotic herbivore (even if that herbivore has very large fitness consequences) because the cue of the exotic herbivore resembles the cue of a native herbivore that has little effect on plant fitness. Evolutionary history of competition should also be important. If two plant species pay the same fitness cost for undefended attack, the plant species that experiences higher fitness costs of unnecessary defense (i.e., the plant with an evolutionary history of strong competition) is expected to induce defenses at a greater amount of the same cue of herbivory risk.

Ecological context should affect allocation. EMT predicts the evolution of strategies of information use within the lifetime of a plant that minimizes the likelihood of costly defensive errors. EMT suggests that the same cue that triggers defense in environments where competition among plants is low might not trigger defense when competition among plants is greater (i.e., as plants err on the side of undefended attack to avoid the higher cost of an error of unnecessary defense). This prediction could be tested by presenting plants with the same cue of risk (e.g., snail mucus [8]) when the plant is in different competitive backgrounds and quantifying the change in defense induction and overall fitness costs. Similarly, EMT suggests that the ability of a plant to withstand consumption should alter its allocation to defense. For example, as discussed earlier, similar concentrations of risk cues should have a greater impact on seedlings than on adult plants. Information regarding the stage of attack should also be important: physical damage and herbivore saliva should trigger a greater response than volatiles from a wounded neighbor. Information about temporal dynamics is also important: a previous attack on a plant is likely to provide considerable information about future risk [9], increasing the likelihood of false-negative errors for plants that do not defend following the initial attack. This can help to explain observations that plants are quick to induce defenses (reducing false-negative error) but slow to relax them following induction (increasing false-positive error) [12].

Allocation to defense should also be affected by the nature of the consumer community, especially when consumers interact in ways that change the costs of errors. For example, if defending against a generalist herbivore makes a plant more attractive to a specialist herbivore, then attracting the specialist becomes a potential cost of unnecessary defense against the generalist. Under these conditions, EMT predicts that the plant might adopt a more stringent decision threshold for allocating to defense against the generalist. Spatial considerations can also influence responses: a plant under attack by root herbivores should require greater evidence of strong aboveground herbivory before translocating compounds from leaves to roots. Interactions could occur in the context of within-organism defenses, for example, plants with information regarding likely attack by microbes should require more evidence that herbivore attack is underway before allocating to herbivore defense. Such covariance among types of errors in multi-consumer situations can help explain why costs of defense can be more apparent in situations where plants are attacked by multiple consumers [12].

EMT helps unify plant defense with other fields where information and risk are studied

By considering plant defense in light of EMT, potentially fruitful links with other disciplines emerge. EMT could be linked with foraging and refuge-use models in animal behavior [7], for example, to explain if and when plants should induce translocation of important compounds to areas where attack is less likely. Models for understanding organismal responses to rapid environmental change often incorporate components of EMT [11]; evaluating plant defense in light of rapid environmental change might have important consequences for conservation of rare plants as well as improved yield of agricultural crops attacked by herbivore pests. It is also possible that different EMT strategies are relatively fixed within a plant species (e.g., risk-prone and risk-averse plant strategies). If so, the existence of alternative error-bias strategies within a population would explain the high levels of variation in defense often observed among individuals [12], and might provide insights for plant and animal defense akin to those derived from the study of behavioral syndromes in animals (see references in [11]).

Concluding remarks

Explaining variation in patterns of plant defense is a primary goal of those who study the ecology and evolution of plants and herbivores. EMT provides an explanation of variation in defense that explicitly incorporates asymmetrical costs of defense and the reality of uncertain, probabilistic attack. Predictions can be tested by incorporating data regarding evolutionary history and costs of different types of errors into observational analyses and meta-analyses. Predictions can also be tested by experiments that manipulate resources and risk of attack. Future work incorporating EMT and other components of signal detection theory (e.g., differences in detectability, classification after detection) might further reveal how present plant defense, similar to so many other phenomena, is shaped by costly events that lie in the past.

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