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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).

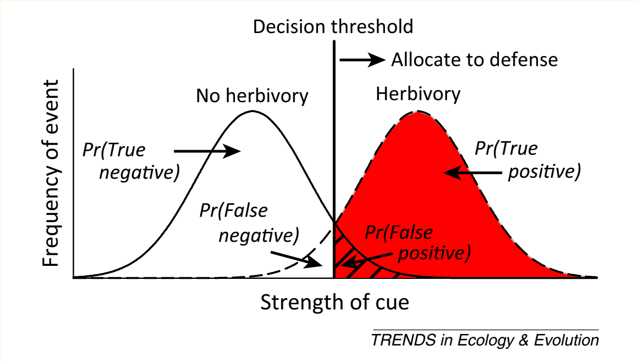

Figure I. When information (e.g., a cue from the environment) can be used to reduce uncertainty regarding attack, false-negative and false-positive errors in defense allocation are important components determining the optimal level of a cue where defense should be initiated. This decision threshold (D) 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