Received: 5 February 2025 | Revised: 12 November 2025 | Accepted: 23 January 2026

DOI: 10.1002/ecy.70355

CONCEPTS & SYNTHESIS

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Associational effects need to be studied within an optimal foraging framework

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Handling editor: Elizabeth Borer

Abstract

In the field of plant–herbivore interactions, a key question is to understand which plants will be consumed. From the point of view of herbivores, this question takes the form of how animals select resources. To answer it, the theory of optimal foraging provides a mathematical framework that takes into account the constraints experienced by animals, such as the availability and diversity of resources available. Historically, plant-focused researchers have framed this question slightly differently: How to explain patterns of herbivory? Hypotheses grouped under the term associational effects aim to describe how plant community characteristics influence these patterns. Results of associational effects studies, however, are variable in magnitude, in direction and are often idiosyncratic. There is a growing awareness that associational effects could be equally well explained by optimal foraging. Several studies of associational effects, however, fail to consider factors linked with herbivores' active foraging choices such as the effects of plant size. I will try to mend the gap between fields using examples of optimal foraging framework integration in studies of associational effects, mostly with mammalian herbivores, but also with invertebrates. I review the proposed mechanisms for associational effects and evaluate whether they could be explained by optimal foraging. Finally, I propose guidance on predictions and type of studies that allow us to discriminate associational effects produced by optimal foraging from other potential mechanisms. Incorporating active foraging choices and using an optimal framework could improve our understanding of associational effects and their variations. Moreover, clearly identifying herbivores as the actor in these interactions forces us to consider their abilities and behavior. It also creates links with nutritional ecology, landscape ecology, and population dynamics and has potential implications in conservation and management practices.

KEYWORDS

diet selection, facilitation, herbivory, neighborhood effect, resource selection

INTRODUCTION

The study of plant–herbivore interactions is at the confluence of multiple scientific fields and involves researchers specialized in diverse organisms: vertebrate and invertebrate herbivores, but also plants. This diversity of expertise can lead to the simultaneous development of animal- and plant-focused hypotheses attempting to explain the same pattern. In an era when online global databases were not present, entire fields emerged and coexisted without connecting and influencing one another. Consequently, new ideas and key findings have been overlooked, with direct consequences on our understanding of plant–herbivore interactions.

A central question in this field is to understand which plants are consumed. From the point of view of herbivores, this question takes the form of how animals select resources. Vertebrate-focused researchers have developed the theory of optimal foraging which explains how animals select resources while balancing nutritional (e.g., pregnancy and lactation) and environmental constraints (e.g., resource availability, thermoregulation; MacArthur & Pianka, 1966, Charnov, 1976). Hypotheses falling under the umbrella of the optimal foraging theory aim to describe animal decisions, with the overarching concept that animals maximize their fitness via optimal food selection. For example, they can maximize the acquisition of energy, or minimize the time spent feeding (Pyke et al., 1977). Modern iterations drift away from optimality, which is difficult to evaluate in natural systems (Railsback, 2022), or are integrated in a larger framework of nutritional ecology (Balluffi-Fry et al., 2022; Raubenheimer et al., 2009). The general concept remains, that is, animals aim to make the best food choices among the resources available.

For plant- and invertebrate-focused researchers, the same question has historically been framed slightly differently: How to explain patterns of herbivory? Multiple hypotheses aim to describe how plant community characteristics influence the probability and amount of herbivory (Atsatt & O'Dowd, 1976; Tahvanainen & Root, 1972). These hypotheses are called associational effects and predict how damage on a focal plant (the study subject) is modified by the presence of a neighboring plant of a different species or phenotype. Neighboring plants can increase (associational susceptibility) or decrease consumption (associational resistance). First developed with invertebrate herbivores (Atsatt & O'Dowd, 1976; Tahvanainen & Root, 1972), these hypotheses are contemporary to the emergence of the optimal foraging theory, mostly developed with mammalian or avian model species (Charnov, 1976; MacArthur & Pianka, 1966; Pyke et al., 1977). Associational effects are now being studied with a wide range of herbivores in various terrestrial ecosystems (Barbosa et al., 2009; Champagne et al., 2016) and, to a lesser degree, in aquatic ecosystems (e.g., Loffler et al., 2015; Wahl & Hay, 1995).

There is a growing awareness that associational effects could be equally well explained by optimal foraging hypotheses (Champagne, Moore, et al., 2020; Miller et al., 2007; Miranda et al., 2011). However, several associational effects studies still fail to consider factors linked to foraging such as focal plant size (Barbosa et al., 2009) or the importance of distinguishing neighboring plants' frequency and density (Underwood et al., 2014). Failure to consider these factors could explain why reviews and meta-analyses of associational effects find variable, opposite, or idiosyncratic results among and within systems (Barbosa et al., 2009; Champagne et al., 2016; Hambäck et al., 2014). In this context, it appears necessary to formally explain how most of the hypotheses for associational effects can be framed as optimal foraging hypotheses and how a foraging framework could provide the unifying background necessary to understand herbivory patterns. In this proposition, a "foraging framework" is defined as a framework that considers the active food choices made by animals.

Foremost, the generally accepted definition of associational effects as a pattern generated by the presence and abundance of alternative food items (plants or phenotypes, Underwood et al., 2014) is a rewording of optimal foraging hypotheses with a plant focus. Actually, most of the proposed mechanisms for associational effects can be defined in an optimal foraging framework (Miller et al., 2007), where the profitability of the focal plant as a food item is influenced by the presence of other items (Table 1). Some mechanisms, however, are harder to fit in this framework and could be used as alternative hypotheses to optimal foraging. In particular, their transferability from invertebrates to vertebrates needs to be tested. For example, under the reduced apparency hypothesis, the neighboring plant provides a certain concealment to the focal plant, thereby reducing the risk of being consumed. Tahvanainen and Root (1972) proposed this mechanism after finding that tomato (*Lycopersicon esculentum*) and ragweed (*Ambrosia artemisiifolia*) release volatile chemicals that hindered the crucifer flea beetles (*Phyllotreta cruciferae*) capacity to find their host plant. Visual concealment is also possible; oak saplings (*Quercus robur*) taller than their neighbors presented higher levels of leaf miners infestation (Castagneyrol et al., 2013). The role of apparency in plant susceptibility to herbivory rests on the sensory acuity and cognitive abilities of the herbivore, an area in which invertebrate and vertebrate herbivores might differ considerably. Moreover, this perceived protection of the focal plant is hard to disentangle from foraging optimization, partly because the characteristics required to conceal a plant covary with factors related to resource quantity and quality (Table 1). In this context, is the protected plant really hidden or are herbivores simply choosing not to consume it?

Using an optimal foraging framework could allow us to answer this question and improve our mechanistic

TABLE 1 Mechanisms for associational effects as listed in Barbosa et al. (2009) and their alternative explanation with optimal foraging.

Mechanism	Source and/or noteworthy examples	Alternative explanation with optimal foraging?
Attractant plant: The neighboring plant is a preferred resource, thus either protecting the focal plant because herbivory is concentrated on the neighbor (decoy plant) or increasing its susceptibility because it attracts herbivores in the vicinity (spillover effect).	Seminal paper of Tahvanainen and Root (1972) is generally cited as the first demonstration of decoy plant (agricultural example with invertebrate herbivore). An example of spillover effect is described in White and Whitham (2000) also with an invertebrate herbivore.	Yes: Directly linked to the concepts of patch selection processes, where the neighboring plant being a preferred resource changes patch quality and thus prediction regarding patch selection and selection within patches, foraging time, giving-up density, and so forth (Charnov, 1976).
Attraction of natural enemies: The neighboring plant attract parasitoids or predators of the herbivores, thus reducing herbivory on the focal plant.	Presented in Root (1973), meta-analysis by Stemmelen et al. (2022) for invertebrate herbivores which found only partial support.	Not directly, when considering the numerical response. A reduction in herbivores number by predation can indirectly affect resource availability. Yes, when considering the effect of risk of predation on foraging. Models addressing the impact of risk on foraging could be used (Brown et al., 1999, Hernández & Laundré, 2005).
Reduction in apparency: The neighboring plant camouflage the focal plant, reducing the ability of the herbivores to detect and consume the focal plant or preventing detection altogether. Camouflage may be olfactive and/or visual.	Reduction in apparency is at the root of the associational effect hypothesis (Atsatt & O'Dowd, 1976, Feeny, 1976), although more recent demonstration exists (Castagneyrol et al., 2013) and it was reviewed by Smilanich et al. (2016) for invertebrate herbivores.	Possibly: Reduction in apparency often covaries with change in relative abundance of resources and thus could be explained by patch selection process (Charnov, 1976). For example, plant size is correlated to the amount of resource available for an herbivore. Reduction in apparency could also be linked to the process of resource detection and giving-up time. Total concealment is harder to place in the framework.
Repulsion: The neighboring plant is repulsive and or toxic to the herbivore, thus providing a haven for the focal plant.	Termed 'repellent neighbors' by Atsatt and O'Dowd (1976), although this concept also included the mechanisms of reduction in accessibility and in apparency.	No, if the mere presence of the neighboring plant is repulsive to the point that a generally consumed food item is avoided. Herbivores can learn to recognize toxic food item (Provenza et al., 2000) and toxicity would need to occur without consumption. Yes, if the presence of a toxic plant modifies patch profitability, thus making this mechanism covered by concepts of patch selection process (Charnov, 1976).
Reduction in accessibility: By its presence and/or physical defense, the neighboring plant reduce the access to the focal plant.	Spines are well known to reduce herbivory by large mammalian herbivores (Cooper & Owensmith, 1986) and can generate associational effects, although spiny shrubs do not provide total protection (Baraza et al., 2006).	Yes: As spines do not provide a total protection, we deduce they increase the handling time for the protected focal plants, thereby affecting its value for the herbivore (Pyke et al., 1977).
Relative abundance of focal and neighboring plant: The effect of the relative concentration or intensity of traits affecting herbivores generates associational effects (Barbosa et al., 2009). It could also be thought of as a numerical effect of resource	First named example in Otway et al. (2005) for an invertebrate herbivore and fundamental framework presented in Underwood et al. (2014). See also Bergvall et al. (2006) for extension to relative palatability of neighbors. Effects of diversity were frequently evaluated for invertebrates	Yes: Directly linked to the concepts of patch selection processes, where the neighboring plant being a preferred resource changes patch quality (Charnov, 1976). The model of Holt and Kotler (1987) for alternative preys (food items) of a same predator (herbivore) are especially relevant here, and similarly

(Continues)

TABLE 1 (Continued)

Mechanism	Source and/or noteworthy examples	Alternative explanation with optimal foraging?
abundance, as defined by Underwood et al. (2014). An extension of this mechanism states that increased diversity reduce damage on focal plants because it reduces the concentration of preferred species (Castagneyrol, Jactel, et al., 2014).	(Castagneyrol, Jactel, et al., 2014, Castagneyrol, Regolini, & Jactel, 2014) but there are a few studies for mammalian herbivores (e.g., Champagne, Dumont, et al., 2018, Vehviläinen & Koricheva, 2006).	relevant models are reviewed in Underwood et al. (2014).
Competition: Competition for resources between neighboring and focal plant change their size or nutritional value, thus changing herbivory rate on the focal plant.	Presented in Barbosa et al. (2009), but this mechanism is said to be hard to discriminate from herbivory, as herbivory affects competition between neighbors by reducing the biomass of one competitor.	Yes: Changes in relative abundance or nutritional value of resources are covered by optimal prey selection and nutritional frameworks (Pyke et al., 1977, Raubenheimer et al., 2009) or at a larger scale, by patch-level selection hypotheses (Charnov, 1976).
Induction of focal plant defenses: Volatile compounds produced by the neighboring plant induce chemical defense in nearby focal plant.	Several examples with invertebrate herbivores presented in Barbosa et al. (2009).	Yes: Changes in relative abundance or nutritional value of resources are covered by optimal prey selection and nutritional frameworks (Pyke et al., 1977, Raubenheimer et al., 2009).
Alteration of abiotic conditions (e.g., soil macronutrients, microclimate): The neighboring plant modifies the environment, indirectly influencing the nutritional value or defense compounds of the focal plant.	Examples presented in Barbosa et al. (2009) support the possibility for an alteration of conditions but are not direct demonstration of associational effects with this mechanism.	Yes: If the alteration of abiotic conditions modifies the quantity or nutritional value of the focal plants, these associational effects could be described by models of optimal prey selection (Pyke et al., 1977) and nutritional models that can handle the complexity of variation in food quality (Raubenheimer et al., 2009).

Note: Mechanisms are roughly ordered by year of first description. Focal plant: the plant for which herbivory occurrence and intensity is assessed.

understanding of associational effects, by creating testable predictions. Unexplained variations in associational effects among ecosystems could make more sense when considered under a foraging framework. A mechanistic understanding of associational effects could also help provide definitive answers regarding the effect of plant diversity on herbivory (Castagneyrol, Jactel, et al., 2014; Castagneyrol, Regolini, & Jactel, 2014; Hambäck & Beckerman, 2003). Additionally, using an optimal foraging framework allows us to put the herbivore as the actor, and forces us to consider its abilities in detecting and selecting resources (Stutz et al., 2015). Finally, considering foraging as the driving force of associational effects creates links with nutritional ecology, potentially allowing for a better understanding of plant–herbivore relationships at large spatial scales (Balluffi-Fry et al., 2022) but also across time, in the context of changing ecosystems. In turn, this has implications for our understanding and predictions of plant and herbivore population dynamics, and the development of ecological communities. In a conservation or management context, we could manipulate the foodscape (quantity, quality and distribution of food, sensu Searle et al., 2007) or the fearscape (spatial distribution of perceived predation risk sensu Brown et al., 1999) to influence foraging behavior, with the aim of improving the establishment of at-risk and/or desired plants. This has been proposed in the associational effect literature, in the form of using shrubs as appropriate microsites for seedling plantations (e.g., Jensen et al., 2012; Mackenzie & Keith, 2009). For this purpose, however, a false understanding of how damage from herbivores varies can lead to failures.

Here, I aim to mend the gap between fields by demonstrating that most associational effects are best explained by foraging. I will focus on terrestrial mammalian herbivores because of the availability of studies discussing associational effects explicitly within an optimal foraging framework for these herbivores, but I will also consider studies with invertebrate herbivores. First, I review demonstrations of associational effects using this framework. Then, with the apparency mechanism as an example, I highlight how difficult it is to distinguish it from optimal foraging. Finally, I propose guidance on how to disentangle potential mechanisms for associational effects.

ASSOCIATIONAL EFFECTS AS A RESULT OF OPTIMAL FORAGING

Approximately 30 years after the seminal mention of associational effects, researchers started to make a connection with optimal foraging. Milchunas and Noy-Meir (2002) explained associational resistance as dependent on both foraging behavior and relative plant palatability ("*an 'unintentional hiding' rather than direct protection*"). Underwood et al. (2014) provided a structuring framework for associational effects that included key foraging concepts: plant population dynamics (i.e., forage availability), density and frequency of focal plant and their neighbors, state of the herbivore, herbivore population dynamics, and patch-level properties. Finally, Hambäck et al. (2014) presented a model of associational effects accounting for patch detection, composition, and scale. The following review will highlight some of the demonstrations of associational effects within an optimal framework using empirical data. It is not exhaustive, but it relies on articles reviewed in a previous meta-analysis for large mammalian herbivores (Champagne et al., 2016). I will roughly follow the steps of optimal foraging, as presented by Pyke et al. (1977): (1) Optimal diet selection; (2) Patch choice and allocation of time to patches; (3) Foraging path.

Optimal diet selection

The key element for incorporating optimal diet selection into associational effects is acknowledging that not all neighboring plants are of equal value. Selection of a diet boils down to what food items are consumed based on their nutritional value, and the searching and handling time required to acquire and consume them (Pyke et al., 1977). It is rather complex to evaluate nutritional value (but see Felton et al., 2018, Stolter, 2018), and we often rely on evaluating selection (i.e., consumption as a function of availability) as a proxy of preference (i.e., selection in the face of equal abundance of multiple food items, Johnson, 1980). For invertebrates, it can also be assessed by the herbivore population dynamics metrics such as population numbers or reproduction rates (e.g., Underwood et al., 2011). Selection or preference has been well integrated in studies of associational effects (e.g., Baraza et al., 2006; Bergvall et al., 2006; Bergvall et al., 2008). For example, in a study of white-tailed deer (*Odocoileus virginianus*) browsing, Minette et al. (2022) discovered that browsing intensity on the less selected post oak (*Quercus stellata*) increased when neighbors of other species were more abundant, but only of species more selected than oaks.

It is not only a question of considering difference among plant species, but also assessing the effect of variations in nutritional value within a species. For example, Moore et al. (2010) demonstrated the effects of eucalyptus size and palatability on susceptibility of their neighbors to koala (*Phascolarctos cinereus*) by mapping intraspecific variation of eucalyptus in formylated phloroglucinol compounds and nitrogen. Many other examples can be found for mammals (e.g., Champagne, Moore, et al., 2018; Champagne, Moore, et al., 2020; Holík & Janík, 2022; Miller et al., 2007), but this has also been extensively considered for invertebrates (e.g., Hambäck et al., 2010; Underwood, 2004; Underwood et al., 2011). It is actually the only variation in nutritional value that matters for monophagous invertebrates. For example, apterous strawberry aphids (*Chaetosiphon fragaefolii*) are specialist herbivores of strawberry plants (*Fragaria chiloensis*) whose movements are influenced by their host plant genotypes but also by the mixture of genotypes (Underwood et al., 2011).

While food item value is of crucial importance, searching and handling time also influence diet selection. Courant and Fortin (2010) evaluated how the energy maximization by bison (*Bison bison*) generated associational effects. The relative palatability of focal and neighboring plant influenced handling time; avoiding a less profitable plant of the same size as its neighbor takes more time and decreased the instantaneous rate of energy intake. It is thus more profitable to consume both plants in a single bite (associational susceptibility). This example includes mathematical notions of maximization but also considering how plant traits influence handling time and search behavior (see also Bergvall et al., 2008 for an experiment manipulating handling). As for the effect of neighbors on search time, neighboring plants could increase or decrease the search time for the focal plant (e.g., reduction in accessibility, Table 1), but very few studies investigated this aspect for vertebrates. Stutz et al. (2015), with videos and assessments of the occurrence of browsing on a weekly basis, demonstrated that neighboring plant species and phenotype affects the herbivore search process, thereby delaying herbivory on the focal plant. Studies regarding search process have been made with invertebrates, although not via a time assessment of search (Hambäck et al., 2003; Hambäck et al., 2010; Underwood et al., 2011). Modification of search time is actually a potential confounding factor in associational effects by reduction in apparency (Table 1).

Patch choice and time allocation

How herbivores select resources in and between patches of resources and decide when to leave a patch for another has been the focus of many studies in optimal foraging (Brown, 1988; Charnov, 1976) but also of associational effects studies. In a series of experiments with fallow deer and pellets or branches of varying quality, Bergvall et al. (2006) have compared associational effects within and among patch (see also Bergvall et al., 2008; Rautio et al., 2008). Hahn and Orrock (2016) manipulated patch density and quality to study the foraging behavior of grasshoppers (*Melanoplus angustipennis*) and the resulting associational effects on *Solidago* spp. Within patch dynamics have also been studied with multiple small and large vertebrates (Champagne, Dumont, et al., 2018; Champagne, Moore, et al., 2020; Emerson et al., 2012; Miller et al., 2007; Miranda et al., 2011; Wang et al., 2010). The takeaway from this abundant literature is rather simple and in agreement with optimal foraging theory: changing patch profitability changes consumption within the patch. When focusing on the resulting occurrence and rate of herbivory for a focal plant species, this result in either an increased (associational susceptibility) or a reduced (associational resistance) rate of herbivory.

Far less attention has been given to time spent in patches and behavior in patches, probably because most of the studies of associational effects measured herbivory once it is realized and did not assess behavior. Theoretically, an animal should leave a patch when the consumption rate in the patch reach the mean rate for the habitat (Charnov, 1976). This prediction relies on the concept that the longer the animal stays in a patch, the more time it takes to find and acquire acceptable food items (the patch is depleted). This has been translated into the concepts of "giving-up time" and "giving-up density" (i.e., the amount of resource left when the animal leaves), that can be used to quantify associational effects (e.g., Emerson et al., 2012). In a similar vein, herbivore selectivity indices, which measures the relative preference for resource items, can be used to link behavior to associational effects (Champagne, Dumont, et al., 2018; Emerson et al., 2012; Wang et al., 2010). For invertebrates, the higher movement rates of strawberry aphids within tricultures compared to monocultures can generate associational effects; aphids were more likely to leave the least profitable genotype of strawberry plant when other genotypes were present (Underwood et al., 2011). Still, there is a need for more assessment of herbivore behavior during the patch foraging process, as these assessments can integrate the effects of additional factors that affect behavior and the resulting associational effects, such as predation risk (Champagne, Perroud, et al., 2018) or social behavior (Stutz et al., 2018).

Foraging path or scaling up the foraging process

Several studies, mostly published after 2010, consider the effects of landscape characteristics on associational effects generated by large herbivores (Champagne, Moore, et al., 2018; Champagne, Moore, et al., 2020; Herfindal et al., 2015; Minette et al., 2022). In a meta-analysis of associational effects with deer-sized herbivores, I investigated how the scale considered (patch size or distance between focal and neighboring plant) affected the strength and type of associational effects (Champagne et al., 2016). Although associational effect strength decreased with scale, some studies present effects of neighboring plant on focal plant herbivory at large distances (kilometers; e.g., DeGabriel et al., 2011, Herfindal et al., 2015, Moore et al., 2015). Such large-scale associational effects can be explained by the spatial hierarchy of foraging decisions (Johnson, 1980) or by effects on herbivore population dynamics when considering invertebrates (Hambäck & Beckerman, 2003). Studies using spatially explicit analyses integrating landscapes features exist, although they are not always categorized as "studies of associational effects." For example, Widén et al. (2024) evaluated the effect of crop type on browsing realized in nearby forest stands in an agro-forested landscape. High-quality crops (oats) increased the browsing on woody plants (associational susceptibility), potentially because cervids needed to balance the high intake of energy by fiber intake. Not only is this study spatially explicit, but it is also nutritionally explicit, and identifies mechanisms of changes in herbivory that could be modulated to reduce risk of herbivory for desired forest regeneration.

APPARENCY AS A MECHANISM FOR ASSOCIATIONAL EFFECTS WITH MAMMALIAN HERBIVORES: EVIDENCE AND ISSUES

Several studies proposing that neighboring plants can mask (visually or olfactory) the focal plant lack the design to exclude the alternative effect of neighbors on the profitability of the focal plant as a food item. For example, Jensen et al. (2012) demonstrated that shrubs reduced browsing on oak seedlings by cervids (*Alces alces* and *Capreolus capreolus*), but especially for seedlings located within the shrubs. In this study, the consideration of relative height and position of the neighboring and the focal plant supports concealment by the neighboring plant. This demonstration, however, lacks an evaluation of the relative profitability (nutritional value and handling time) of the resources and thus cannot exclude that the observed effect is due to optimal foraging. Taller seedlings are easier to manipulate and provide more resources to large herbivores, which could explain the higher browsing frequency and intensity of seedlings relatively larger compared to their neighboring shrubs. Other studies found reduced herbivory for smaller focal plants in the presence of taller neighbors (Akashi et al., 2021; Pietrzykowski et al., 2003) but fail to account for the effect of size on manipulation and forage quantity. Similarly, in the relation between oak apparency and leaf miner infestation in Castagneyrol et al. (2013), oak quality was not assessed and could have generated the associational resistance. The study of Courant and Fortin (2010) described in the previous section demonstrates that considering the effects of relative plant size on forage handling and the resulting energy gains can explain associational effects without invoking a reduction in apparency.

Studies proposing a reduced apparency mechanism outside of a foraging framework can also fail to detect associational effects because factors with a strong influence on foraging were not considered. Considering several neighboring plants to be of equal value can preclude the identification of associational effects. For example, Betras et al. (2022) proposed that shrubs producing a dense cover could provide a refuge from browsing to other plants by reducing their detectability. No statistically significant associational effect was found in this study, probably because several non-native shrubs were present and grouped in analyses. The authors recognize this issue and propose that future studies should integrate difference in palatability of the neighboring plants, alongside deer density and preferences. This issue is not limited to studies of reduced apparency. The study of associational effects considering the effects of diversity would also benefit to define neighborhood in terms of resource (e.g., Castagneyrol, Regolini, & Jactel, 2014).

Predictions based on neighboring plants utterly preventing focal plant discovery are more difficult to understand under an optimal foraging framework and, for vertebrates, could rest on a poor understanding of herbivore foraging. Mammals are good at finding food because of their cognitive and sensory abilities. Most of the time, the apparency of plants to mammalian herbivores is evaluated with human senses and capacity of detection, but what is hidden to us could be very apparent to herbivores. Olfaction, especially, can have a very strong impact on the detection of inconspicuous food resources as all plants produce some sort or another of volatile compounds. Moreover, many volatile compounds reduce nutritional value or are toxic, making them reliable indicators of plant value as a resource (Provenza et al., 2000). Swamp wallabies (*Wallabia bicolor*) use cineole, a widely distributed monoterpene, as a cue to find resources (Bedoya-Perez et al., 2014) and will use olfactory cues in the absence of visual cues (Stutz et al., 2017). African elephants (*Loxodonta africana*) are able to discriminate olfactive cues related to palatable plants in a complex olfactive environment consisting of multiple non-palatable plants; their ability to do so increased with trials (McArthur et al., 2019). Lamb also learned to avoid an odor when it was related to negative post-ingestive cues (Provenza et al., 2000). Learning is an important part of feeding behavior, and mammalian herbivores use long-term memory of events and places to find and consume plants (Ejsmond & Provenza, 2018). This is crucial when considering that a number of mammals feed on woody perennial plants that will be present year after year.

In this context, it seems that it is not a matter of *if* but rather a question of *when* a plant is found. Stutz et al. (2017)'s experimental design disentangled the effects of visual and olfactory cues for wallabies; notwithstanding nutritional value of the plants or their position (upright or pinned to the ground), the number of patches left unvisited by wallabies decreased with time, with very little seedlings left unbrowsed by the end of the experiment (6 weeks). Under a foraging framework, this can be described and predict under the concept of search time, but also of search effort, that can change with herbivore population or resource availability. Surprisingly, the presence of an artificial odor treatment mimicking a plant of low nutritional value can fool African elephant (Finnerty et al., 2024); in the presence of olfactory cues of low food quality, they avoided patches that included their preferred plant. However, only the first choice of the elephants was recorded, and they always had access to the preferred plant without the avoided neighbor presence or without its odor. Rather than an example of olfactory concealment, these results are understandable under an optimal patch selection process (selection of patches with only the preferred resource). In summary, if you wait long enough, there is a strong possibility that preferred plants will be consumed (Pietrzykowski et al., 2003).

DISTINGUISHING APPARENCY FROM OPTIMAL FORAGING

To properly study associational effects, I recommend considering an optimal foraging framework, explicitly assessing variables such as relative plant values, patch profitability, foraging scale, and animal's behavior and abilities. Additional factors influencing foraging, like nutritional state or predation risk, could also be integrated by relying on the already developed concepts and hypotheses. These variables could very well be integrated into empirical work, but even more so in a mathematical model to predict associational effects. Hambäck et al. (2014) proposed such a model for invertebrates, but to my knowledge, it has not yet been adapted to vertebrates.

To test reduction in apparency, we need studies that explicitly evaluate apparency and compare it with the alternative hypothesis that the focal plant is less profitable in the presence of the neighboring plant. These two mechanisms are not mutually exclusive and could both contribute to a reduction in herbivory, but we can test mutually exclusive predictions. If associational resistance is generated by a neighboring plant concealing a focal plant:

1. Associational resistance will remain constant under variation in amount (i.e., size, biomass) or quality (i.e., nutritional value) of the focal plant.

The amount and quality of a food item are tightly linked to its consumption and to the profitability of the patch (Charnov, 1976). If increasing quantity/quality of the focal plant increases its consumption, it would rather suggest that the resource was not concealed; it was simply unprofitable to consume. If, as predicted, the associational resistance is unrelated to the resource value, it suggests that the focal plant is indeed concealed. The challenge is to separate profitability from apparency. A bigger focal plant provides more resources, but it might also be taller than the neighboring plants and thus, more apparent.

2. Associational resistance will remain constant under variation in herbivore nutritional state or resource availability within the herbivore's home range.

When nutritional demands are high (e.g., lactation) or at low resource availability, food items that are generally avoided or are less selected can be consumed (Lashley & Harper, 2012; Sauvé & Côté, 2007). If associational resistance varies with these factors, it implies that the plant was not concealed, simply not consumed in favor of more accessible and more profitable resources. This prediction is more easily tested when the neighboring plants that provide the concealment are completely avoided by the herbivore, as neighbor consumption affects its ability to conceal. Additional factors also need to be controlled to properly discard an effect of plant apparency. For example, herbivore density can modulate resource availability, but higher herbivore density also creates additional encounters between herbivores and plants. If the neighboring plant reduces detection probability, additional encounters could increase herbivory on the focal plant, because of an increase in 'chances' to find the focal plant associated with more 'trials'.

3. Associational resistance will be influenced by the neighbor's traits influencing concealment (e.g., branching patterns or emission of volatile compounds) and with traits related to focal plant detectability (e.g., height relative to the protector or emission of volatile compounds).

It is rather self-explanatory that traits influencing apparency should be the ones that influence the associational resistance generated by reduced apparency. However, as stated above, it is difficult to modify traits affecting the degree of concealment without affecting resource value and vice versa (see Miller et al., 2007 for an example of this issue). Height is a good example of such traits, as a plant overtopping its neighbor is more apparent but generally also provides more resources. Similarly, several volatile compounds affecting apparency contribute to chemical defense and thus reduce the nutritional value or increase its toxicity (Champagne, Royo, et al., 2020).

What are the ideal studies to test these predictions? Experiments, either in a controlled environment with captive animals or in a natural environment, are the first idea that comes to mind because they allow us to dissociate quantity/quality from apparency and to manipulate profitability or number of encounters. Indeed, many discoveries in associational effects were made through experiments (among others Bergvall et al., 2006, Miller et al., 2007, Wang et al., 2010). New advances in laboratory analyses even allow us to manipulate olfactory cues with a high level of realism (Finnerty et al., 2024). As an example to emulate, Miller et al. (2007) proposed *Eucalyptus nitens* of high and low quality to pademelons in different trials: with selected or avoided neighbors, with high or low availability of resources, with short or tall avoided neighbors. These several trials contribute to the understanding of how changes in relative profitability modify *E. nitens* susceptibility to herbivores. In captive experiments, or even in those in natural environments, we can also assess behavior (e.g., Bergvall & Leimar, 2017; Champagne, Perroud, et al., 2018; Stutz et al., 2015), which can help identify the foraging step modified by neighboring plants and potentially determine the contribution of apparency. Moreover, controlling the amount and quality of food provided allows calculation of profitability, of giving-up density, of intake rate, of time spent in patches, and so forth, which allows us to measure and investigate deviations from optimal foraging predictions.

Another possibility is to analyze these interactions in natural environments, with observational studies and/or modelizations using observations as data input. Advancement in statistics, such as path analyses (Shipley, 2013), and model selection and multimodel inference (Mazerolle, 2006) are particularly useful in this context because we need to consider numerous covariates. In the specific example of distinguishing apparency and profitability, we need analyses able to evaluate the relative impact of concealment, forage quantity and quality, and other landscape factors that influence herbivore foraging. It is not, however, a question of integrating a bunch of variables in a trendy statistical method. A careful selection of relevant variables and how to measure them is required because, again, herbivores are the actors generating the patterns. Their abilities and their behavior need to guide our investigations.

CONCLUSION

When considering the herbivory risk for a specific plant, how can we say if herbivores are not detecting it or just choosing not to consume it? I propose that mammalian herbivores may just be choosing not to consume the plant, as the effects of neighboring plants on the consumption of another plant may be better explained by foraging optimization. By being mindful of this nuance, we will design studies better apt at understanding plant–herbivore interactions. This knowledge will allow us to make predictions regarding herbivory that will stand the test of time and of variation within and among systems.

Considering herbivores' active foraging choices properly when explaining patterns of herbivory is an idea that has been progressing in the 21st century outside of its traditional field of optimal foraging, for all types of herbivores. Placing the herbivore as the actor of associational effects brings us closer to the mechanism behind a pattern, and thus to an understanding of natural processes. It is also about working together, across systems and organisms types, on questions with potential conservation and management implications.

ACKNOWLEDGMENTS

This work started when Jean-Pierre Tremblay found my thesis introduction boring. I am grateful to him for the initial push to think, integrate and reflect critically. My thesis evaluation committee, Steeve Côté, Monique Poulin, Nora Underwood, and Daniel Fortin, also provided valuable comments and challenging questions that refined my ideas. Thanks to Alex Royo, Olivier Villemaire-Côté, and François Hébert for the feedback and encouragement and to two anonymous reviewers and to editors at *Ecology* for revising previous versions of the manuscript.

CONFLICT OF INTEREST STATEMENT

The author declares no conflicts of interest.

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How to cite this article: Champagne, Emilie. 2026. "Associational Effects Need to Be Studied Within an Optimal Foraging Framework." *Ecology* 107(3): e70355. https://doi.org/10.1002/ecy.70355