Title: Fruit Secondary Metabolites Shape Seed Dispersal Effectiveness

Authors:

Nelson, Annika S.*

Whitehead, Susan R.

Affiliation and address of both authors:

Department of Biological Sciences, Virginia Polytechnic Institute and State University, Derring Hall Room 2125, 926 West Campus Drive, Mail Code 0406, Blacksburg, VA 24061

Emails and ORCIDs:

* Corresponding author: Annika S. Nelson, annikasn@vt.edu, 0000-0002-1086-0077

Susan R. Whitehead, swhitehead@vt.edu, 0000-0002-7089-4594

Websites and Twitter Handles:

https://annikanelson.weebly.com/, @AnnikaSNelson

http://www.speciesinteractions.com/, @WhiteheadLabVT

Keywords: Chemical ecology; fruit defense; plant secondary metabolites; specialized metabolites; seed dispersal effectiveness

Abstract

Plant secondary metabolites (PSMs) play a central role in seed dispersal and fruit defense, with potential for large impacts on plant fitness and demography. Yet because PSMs can have multiple interactive functions across seed dispersal stages, we must systematically study their effects to determine the net consequences for plant fitness. To tackle this issue, we integrate the role of fruit PSMs into the seed dispersal effectiveness (SDE) framework. We describe PSM effects on the quantity and quality of animal-mediated seed dispersal, both in pairwise interactions and diverse disperser communities, as well as trade-offs that occur across dispersal stages. By doing so, this review provides structure to a rapidly growing field and yields insights into a critical process shaping plant populations.

Highlights

- Secondary metabolites in fruits can shape plant fitness and demography by mediating interactions with both antagonists (seed predators and pathogens) and mutualists (seed dispersers).
- The effects of fruit secondary metabolites on the outcome of seed dispersal can be described using the seed dispersal effectiveness framework, which quantifies the number of new adult plants produced through the activities of a disperser.
- By examining how fruit secondary metabolites not only mediate pairwise interactions but also shape interactions with broad communities of seed dispersers, we describe a wide range of potential effects on plant fitness.
- Because the same metabolites can serve multiple functions across different seed dispersal stages, with the potential for complex trade-offs, examining their effects under multiple contexts is necessary to understand their adaptive significance.

Secondary Metabolites Shape Seed Dispersal and Fruit Defense

Plant secondary metabolites (PSMs) (see Glossary) are incredibly diverse and play a key role in shaping biotic and abiotic interactions [1,2]. Most widely recognized is their fundamental importance to plant defense and plant-herbivore coevolution – a discovery that revolutionized the field of chemical ecology and spawned decades of research [1,3]. A rapidly growing body of evidence is beginning to demonstrate that PSMs also mediate most other species interactions surrounding plants, including animal-mediated seed dispersal [4,5].

PSMs in fruit have been proposed to play multiple adaptive roles in attracting and modifying interactions with **seed dispersers** (Box 1) [6]. Yet PSMs that attract dispersers can also increase vulnerability to **seed predators and pathogens**, and defensive compounds can likewise deter dispersers [7,8]. Perhaps as a result of contrasting selective pressures from mutualists and antagonists or pleiotropic effects [9,10], most fruits contain diverse mixtures of attractive and defensive PSMs [11,12]. Although the identities and functions of the majority of fruit PSMs are not yet known, field experiments coupled with quantitative chemical analyses have greatly advanced our understanding of the ecological effects of a variety of compounds in fruits [5,7,13]. However, because many PSMs serve multiple functions and can act synergistically or antagonistically with other compounds [14,15], evaluating their net effects on plant fitness remains challenging.

Seed dispersal effectiveness (SDE) is a widely used conceptual framework for evaluating the outcome of animal-mediated seed dispersal [16,17]. SDE is calculated as **seed dispersal quantity** multiplied by **seed dispersal quality**. This framework has yielded great insight into many factors that determine the outcome of animal-mediated seed dispersal. Most frequently, it is applied to assess variable contributions of different frugivores to a plant’s overall fitness (e.g., [18,19]), which can be quantified and visually compared using **SDE landscapes** that plot dispersal quantity against quality [16].

While multiple plant traits are important for mediating seed dispersal [4,20,21], relatively few studies have investigated how inter- or intraspecific trait variation of plants themselves influences SDE (but see studies of the role of fruit crop, fruit, and seed size [22]). In this paper, we integrate PSMs into the SDE framework to demonstrate how to systematically evaluate their fitness effects in the context of animal-mediated seed dispersal. We focus on biologically active PSMs in fruits because (1) they can have broad effects on all stages of animal-mediated seed dispersal and (2) the SDE framework can conceptually unify research on the chemical ecology of seed dispersal.

Secondary Metabolites Mediate the Effectiveness of Individual Seed Dispersers

PSMs can alter SDE by influencing both the quantity and quality of services a disperser provides to a plant (Fig. 1, Box 2). The composition of biologically active PSMs, both within and across fruits, can influence seed dispersal <u>quantity</u> through effects on (1) the number of disperser visits and (2) the number of seeds dispersed per visit. Such effects occur when PSMs directly attract, reward, deter, or convey information about fruit quality to dispersers, or indirectly mediate the effects of other biotic or abiotic factors on fruit availability and quality. For fruits that are removed, PSMs can influence seed dispersal <u>quality</u> by altering (1) the **quality of seed handling** and (2) the **quality of seed deposition**, through effects on disperser behavior or physiology. Below, we detail how fruit PSMs influence each SDE component.

<u>Seed Dispersal Quantity</u>

Number of Disperser Visits

Fruit availability and quality can play a strong role in determining the number of disperser visits to a plant. PSMs that influence fruit availability or quality by mediating interactions with pests or pathogens can thereby indirectly affect disperser visitation (Fig. 1A). Because many pests decrease fruit availability or quality [23], PSMs that prevent fruit attack can indirectly increase disperser visitation. Such effects may be especially pronounced if PSMs extend fruit persistence later in the growing season when other fruits have become scarce, increasing their relative value [24]. Conversely, when pests or pathogens increase fruit quality or attractiveness, such as when fungal pathogens increase the production of attractive volatiles emitted from fruits [25], PSMs that defend against antagonists may indirectly decrease disperser visitation.

In fruits present, PSMs that determine fruit color, odor, and flavor can be general attractants that allow a disperser to detect and decide to visit a plant (Fig. 1B) [26,27]. Fruit color is typically composed of PSMs that act as pigments, such as carotenoids, flavonoids, and betalains [28], that often make fruits more visually conspicuous and can also serve as nutrients for dispersers such as diurnal birds and mammals [27,29]. Fruit odor and flavor consist of tens to hundreds of unique volatile PSMs – primarily terpenoids, fatty acid derivatives, aromatic compounds, and nitrogen- and sulfur-containing compounds – that typically attract dispersers such as ants and mammals [26,30–32]. A plant may receive more visits if it produces many fruits with high amounts of attractive PSMs [27]. A plant could also potentially receive more visits if it produces fruit with more complex blends of PSMs, which may increase their detectability or specificity of signaling (Fig. 1B) if dispersers rely on mixtures of PSMs to select fruits to remove [33].

In addition to serving as general attractants, PSMs can contribute to and signal fruit quality (Fig. 1C). High-quality fruits are those that contain high amounts or diversity of nutritious compounds, including macronutrients (i.e., lipids, proteins, and carbohydrates), micronutrients (i.e., minerals and vitamins), or PSMs that may be directly nutritious or used to self-medicate or reduce parasite loads (e.g., antioxidants, antimicrobial, or insecticidal compounds) [34–36]. High-quality fruits may also contain low amounts or diversity of detrimental PSMs, such as phenolics, sulfur-containing compounds, terpenes, or alkaloids that are unpalatable, toxic, or interfere with digestion [37].

Because PSMs that contribute to fruit odor, flavor, and color are often correlated with both nutritional rewards and detrimental PSMs [34,38,39], they can be honest signals of fruit quality that promote disperser visitation to plants with high-quality fruit (Fig. 1B & 1C) [34,40]. These compounds could also potentially facilitate associative learning, cognitive functioning, or route-finding [31,41,42], further increasing a disperser's visitation to plants with high-quality fruits as it gains experience. Moreover, if a disperser physiologically adjusts to consuming fruits with a particular mix of PSMs [43,44], continuing to consume those same fruits may increase digestive efficiency, potentially even further strengthening the positive effects of learning on fruit removal. Yet a disperser may also become satiated [45] or require different or more diverse nutrients over time [46,47], potentially weakening the positive effects of associative learning. Overall, the role of associative learning in mediating SDE likely depends on a variety of factors, including the strength of the signal and disperser nutritional status [47].

Alternatively, fruit PSMs could increase disperser visitation by being deceptive, addictive, or memory-impairing, thereby tricking naïve and potentially even experienced dispersers into removing low-quality fruits (Fig. 1C). Both olfactory and visual deception occurs in seed dispersal [48]. Examples of olfactory deception include *Ceratocaryum* spp. (a South African sand plain plant) seeds that emit volatiles mimicking herbivore dung, attracting dung beetles to roll and bury them [49], as well as lipid-rich appendages ("elaiosomes") attached to some ant-dispersed seeds that attract ants without providing high-quality rewards in return [50]. Examples of visual deception include mimetic seeds, which resemble fleshy fruits in color but are associated with no or little food rewards [51]. While deception appears to be relatively uncommon compared to honest signaling, the connections between attractants, rewards, learning, and deception and their net effects on seed dispersal quantity present a promising area for future research (see Outstanding Questions).

Number of Seeds Dispersed per Visit

The number of seeds dispersed per visit can depend on PSMs that determine the perceived profitability of a plant's fruits (Fig. 1C, Box 2). The density of fruit remaining on a plant when a disperser decides to leave ("giving-up density" [52]) could be modified by PSMs that alter the relative costs and benefits of searching for new fruit-producing plants versus exploiting the current one. While searching for new fruit-producing plants carries the costs of increased energy expenditure and predation risk, it may be advantageous when a disperser becomes satiated or experiences diminishing returns from continuing to consume a plant's fruits [53]. Thus, any PSMs that increase a plant's perceived fruit value by providing direct rewards, mitigating or improving the effects of other biotic or abiotic factors on fruit quality, extending fruit persistence, or causing deception or addiction (see "Number of Visits") may increase the number of seeds dispersed per visit [53,54]. Likewise, PSMs that decrease perceived fruit value by being generally deterrent or toxic, interfering with digestion, or reducing foraging efficiency can reduce the number of seeds dispersed per visit (Box 1) [5–7,37].

PSM diversity, including both total richness and variability within and among a plant's fruits, could also have important but previously unexplored effects on the number of seeds dispersed (see Outstanding Questions) [2,12]. Because fruits are often nutrient deficient, an animal may remove more fruits if they contain a greater diversity of nutritious or rewarding PSMs that increase their perceived profitability (Fig 1C). PSM diversity among fruits on a plant could also potentially increase the number of seeds dispersed per visit, if by communicating information about variation in fruit quality (e.g., ripeness [55,56]), PSMs facilitate faster removal of a plant's most valuable fruits (and avoidance of the least valuable).

Seed Dispersal Quality

Quality of Seed Handling

After removal, PSMs can modify whether seeds are separated from fruit pulp, ingested, broken, or damaged in a disperser's mouth or gut, with consequences for seed viability (Fig. 1E) and recruitment success (see "Quality of Deposition"). Toxic or distasteful PSMs, for instance, can cause a disperser to drop intact or partially consumed fruits, rather than consume seeds or separate them from fruit pulp (Box 2) [7]. This may dramatically alter SDE because gut passage and pulp removal can increase or decrease the probability of **secondary seed dispersal** [57,58], seed predator or pathogen attack [59,60], and germination [61,62] (see "Quality of Deposition"). PSMs can also prevent would-be seed predators from destroying seeds, instead effectively dispersing them [63,64]. For example, granivorous rodents are more likely to cache (versus consume) nuts and seeds with high tannins and low nutrients, with the potential to later germinate [65,66]. Similarly, although glucosinolates in *Ochradenus baccatus* (taily weed, a Mediterranean shrub) fruit pulp are harmless when intact, they create a "mustard oil bomb" when consumed together with the seeds, which contain enzymes that convert glucosinolates into toxins. To avoid this "bomb," rodents spit out the seeds intact [63].

Fruit PSMs can also influence seed handling quality by modifying the amount of time seeds are retained in a disperser's digestive tract (Fig. 1F, Box 2). PSMs may not only influence retention time by potentially inducing vomiting [67] but can also have laxative or costive effects on non-regurgitated seeds [68,69]. This could alter SDE, since seeds that pass through and are retained longer in the gut typically experience greater seed coat breakage, digestion, and scarification, with variable consequences for germination (depending on seed coat thickness, seed size, and whether gut passage is critical for breaking dormancy) [70,71].

Quality of Seed Deposition

By altering disperser behavior or physiology, fruit PSMs can modify the location or conditions where seeds are deposited that ultimately determine rates of survival and germination (Fig. 1G-1I). Dispersal distance is one of the most widely recognized determinants of seed deposition quality (Fig. 1G). Generally, seed and seedling performance increase with some distance from maternal, conspecific, or closely related plants as a result of density-dependent competition and natural enemy attack [72–74]. Seeds tend to be deposited in aggregations near the maternal plant when they are spat out or regurgitated but deposited farther away in clumps (with mixtures of both con- and heterospecific seeds) when they are consumed and retained longer in the gut [70,75]. Therefore, PSMs can alter dispersal distance by modulating the timing of dispersal [6,13], likelihood of seed consumption and gut passage [7], and gut retention time (see “Quality of Handling”; Fig. 1D-F) [68,69]. For example, amides (nitrogen-based defensive compounds) delay *Carollia* bats from consuming *Piper* (pepper plant) fruits, and as a result of being consumed later at night when bats are less active [13] in combination with the laxative effects of amides [68], seeds are dispersed shorter distances (Box 2) [13].

At a finer scale, PSMs can alter seed deposition microsite, with potential to affect plant fitness (“**directed dispersal**”) (Fig. 1H) [76]. For instance, scatter-hoarding rodents are more likely to deposit highly nutritious seeds under shrubs versus exposed sites (although this does not appear to influence seed or seedling performance) [77]. Similarly, by reducing the likelihood of bats consuming (versus dropping) fruits [7] and the gut retention time of fruits that are consumed [68], PSMs in *Piper* fruits reduce the likelihood of seeds being defecated beneath bat roosts, where the plant may experience increased competition but reduced herbivory [78]. However, compared to other effects on seed dispersal quality, the effects of PSMs are little understood within the context of mediating seed deposition microsite.

Finally, by influencing the number of seeds removed per visit (see “Dispersal Quantity”), PSMs can modify the number of competing seeds deposited together (Fig. 1I). For instance, PSMs that reduce the number of fruits consumed per visit to a plant may simultaneously increase the number of plants a disperser can visit before defecating [79]. While this could provide the benefits of decreased intraspecific competition (especially with seeds from the same maternal plant) and increased seed availability for dispersal by other species (see “Landscapes”), it could also increase the likelihood of depositing a mixed seed load, resulting in high interspecific competition among seeds and seedlings. Some evidence suggests that conspecific (versus heterospecific) seed density has stronger effects on plant recruitment [80], although the net effects of PSMs on SDE in the context of mixed seed loads requires further investigation.

Secondary Metabolites Cause Trade-offs in Dispersal Effectiveness

Because PSMs have contrasting effects on different components of SDE and plant fitness, trade-offs can occur between various ecological effects that contribute to a single SDE component (Fig. 1). Perhaps the most widely recognized trade-off contributing to variation in seed dispersal quantity is the defense trade-off, in which toxic or deterrent PSMs that defend against pre- and post-dispersal seed predators and pathogens increase seed availability (Fig. 1A) but also reduce the attraction of effective dispersers (Fig. 1C; Box 2) [7,14,21]. Plants employ multiple strategies to minimize or escape this trade-off. For instance, plants may avoid producing PSMs in fruits or seeds unless they are slow to be removed and thus more vulnerable to attack, as is the case for mimetic seeds [81,82]. In other cases, defensive PSMs can have targeted effects on natural enemies but no effect on dispersers (directed deterrence hypothesis) [83,84].

A variety of trade-offs can also occur among ecological effects contributing to seed dispersal quality. For example, when PSMs increase gut retention time of seeds, multiple factors contributing to dispersal quality may change in opposing directions. While dispersal distance can increase (positive effect [72,73]), so too may seed coat scarification, breakage, and digestion (positive or negative effect, depending on seed traits [71]) and the number of seeds deposited together (negative effect of competition [79]). As a result, it is important to evaluate and compare the relative importance of multiple ecological effects that contribute to each SDE component and subcomponent (see Outstanding Questions).

Furthermore, fruit PSMs can contribute to trade-offs between SDE components or subcomponents. Quantity/quality trade-offs are likely particularly common. They can occur, for instance, when PSMs induce dispersers to leave earlier in a foraging bout (reducing seed dispersal quantity) but also increase seed dispersal distance and reduce the density of conspecific seeds deposited together (increasing seed dispersal quality) [6]. Due to the difficulties of measuring the effects of PSMs on all ecological effects contributing to SDE, our understanding of trade-offs among different SDE components remains limited. Yet meeting this challenge using long-term studies in model systems will be invaluable for quantifying the net effects of PSMs on plant fitness taking trade-offs into account (see Outstanding Questions).

Secondary Metabolites Structure Seed Dispersal Effectiveness Landscapes

Most plants associate with a wide diversity of seed dispersers that range in effectiveness. Because dispersers differ in morphology, physiology, and behavior, shifts in disperser composition could impact a plant's SDE [18,70], which can be visualized using SDE landscapes (Fig. 2) [16]. The same total SDE can be achieved through multiple quantity/quality combinations along an isocline, and fruit PSMs may shape SDE landscapes in two main ways – by modulating the composition of the animal species in a disperser community [85] and by shifting their relative effectiveness [69] (Fig. 2).

First, PSMs can shift the community composition of seed dispersers through a variety of mechanisms (Fig. 2). Energy-rich fruits are often dispersed by a greater diversity of animals than energy-poor fruits [86]. Broad differences in fruit chemical profiles can also attract different disperser assemblages ("dispersal syndromes"). Bird-dispersed fruits, for example, are typically less odorous, smaller, softer, and more visually conspicuous than mammal-dispersed fruits [4,87]. Toxic or deterrent PSMs can also structure disperser communities when dispersers are differentially sensitive their effects (directed deterrence hypothesis) [6,84]. In the few systems where this has been explored, birds seem to be generally less sensitive to toxins than mammals, as is the case with capsaicinoids in wild chilies (*Capsicum* spp.) [84] and alkenylphenols in *Piper sancti-felicis* [5]. Thus, despite reducing seed dispersal quantity by deterring some animals, seed dispersal quality can increase if the animals that are deterred are the least effective dispersers (see "Trade-offs"). In this way, a plant could potentially use fruit PSMs to manipulate consumer assemblages to its advantage [6,84], warranting further investigation of such effects and the ultimate consequences for plant fitness (see Outstanding Questions).

Second, fruit PSMs could alter the relative effectiveness of the dispersers present. PSMs could potentially affect all seed dispersers equally, shifting total SDE but not the relative positions of dispersers in the SDE landscape (Fig. 2a). However, PSMs are more likely to have different effects on different dispersers, shifting their relative landscape positions (Fig. 2b). Capsaicin in *Capsicum* spp. (wild chilies), for instance, increases the gut retention time of seeds in birds. Yet because its effects are delayed, it only increases gut retention time for birds with already slow passage rates [69]. This could potentially alter relative effectiveness of dispersers, if by increasing retention time, capsaicin increases dispersal distance and seed digestion and scarification for seeds dispersed by some birds but not others. However, compared to effects on the community composition of disperser assemblages, PSM-mediated changes in the relative effectiveness dispersers are little understood.

Concluding Remarks: Towards Quantitative Predictions in Complex Environments

We have outlined multiple ways in which fruit PSMs alter SDE. PSMs have a wide diversity of effects on multiple seed dispersal stages, often resulting in trade-offs and shifts in SDE landscapes. Yet much remains to be learned about many topics, ranging from the net fitness effects and adaptive significance of PSMs in fruit, to the effects of PSM diversity on SDE, and context-dependencies in the production and ecological functions of fruit PSMs (see Outstanding Questions).

To move towards quantifying the net effects of fruit PSMs on SDE and ultimately plant fitness, it is important to assess effects on both dispersal quantity and quality. A first step is to measure the effects of one or a single class of PSMs on the effectiveness of one or a guild of seed dispersers before eventually considering additional ecological complexity. Although SDE subcomponents are quantified differently across systems, it is often relatively straightforward to measure seed dispersal quantity by counting the total number of seeds removed in response to either natural variation or artificial manipulation of PSMs in fruit. However, quantifying PSM effects on seed dispersal quality poses a much greater challenge and to our knowledge has not been comprehensively done. This is in part due to the difficulties of tracking individual seeds from their maternal plant to the deposition site, and of tracking plants throughout their entire lifecycle, from seeds to new adult plants. Yet studies that tackle pieces of this puzzle, even by evaluating just one or several SDE components, can yield great insights.

Because fruits are chemically complex, making quantitative predictions will also require considering how the effects of a particular PSM depend on the surrounding the chemical environment of the fruit [14,15]. For example, defensive PSMs can have weaker or stronger effects in combination and in some cases depend on the identity of the fruit consumer [14]. PSMs with contrasting ecological effects (e.g., attractants versus deterrents) may be particularly promising areas for future focus. [8,83,88,89]. A major future direction should be to evaluate the effects of multiple PSMs both individually and in combination, as well as the effects of PSM diversity itself, on SDE (see Outstanding Questions).

By integrating fruit PSMs into the SDE framework, we hope we have provided insight into how to systematically evaluate the ecological roles of fruit PSMs in the context of animal-mediated seed dispersal. Because the SDE framework is broadly generalizable, it can be extended to include additional plant traits and interactive effects among traits (see Outstanding Questions). Such steps will be key to developing deeper insight into the factors driving variation in seed dispersal, a critical process for structuring and maintaining plant populations.

Acknowledgements

Many thanks to Geno Schupp, Lauren Maynard, Mariana Gelambi Desiato, Melissa Burt, Kendra Walters, Dhruba Banerjee, and three anonymous reviewers for their insights and feedback. This work was funded by National Science Foundation Grant no. 1856776 to SRW.

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Fig. 1. Effects of Fruit Secondary Metabolites on Seed Dispersal Effectiveness

The main components and subcomponents of seed dispersal effectiveness (SDE) [16] can be multiplied together to calculate the number of new adult plants produced as the result of animal-mediated seed dispersal. SDE can be affected by plant secondary metabolites (PSMs) in fruit that perform a variety of functions, which we have divided here into non-mutually exclusive categories based on their potential ecological effects (labeled A-I). All effects contributing to seed dispersal quantity are shown in green, and all effects contributing to seed dispersal quality are shown in blue. Clearly, the same PSMs can perform many functions with effects spanning SDE components. Some factors may be more directly determined by PSMs than others, and some ecological effects may play a more important role in influencing SDE subcomponents than others. Thus, although SDE components and subcomponents are multiplicative, not all ecological effects are necessarily multiplicative.

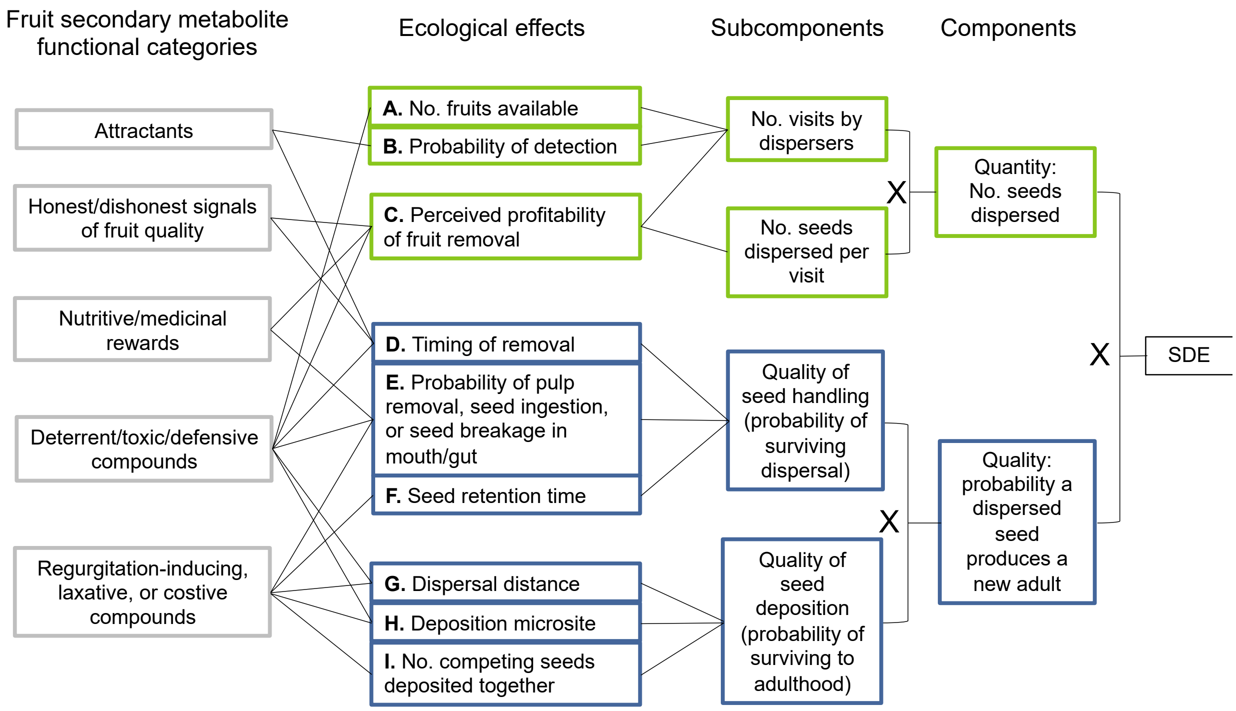
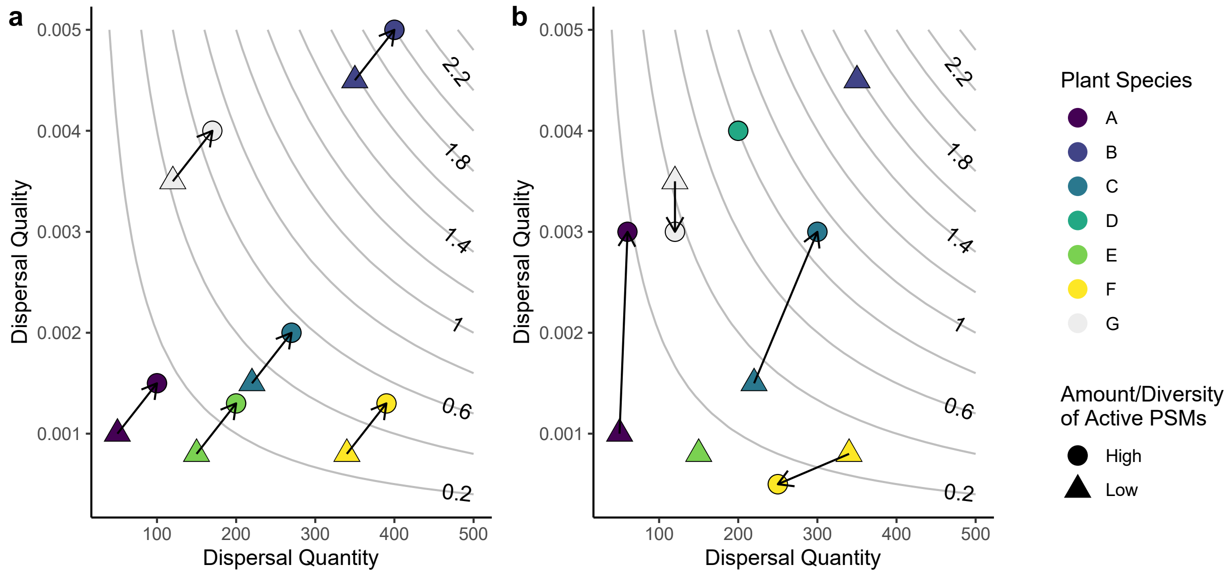


Fig. 2. Hypothetical effects of the amount or diversity of biologically active plant secondary metabolites (PSMs) in fruit on a seed dispersal effectiveness (SDE) landscape. Each point represents the SDE of a different seed disperser species (color), based on its dispersal quantity (x-axis) and quality (y-axis) under either low (triangle) or high (circle) PSM amounts or diversity. Combinations of quantity and quality that lead to equal SDE values (where SDE = quantity x quality) are shown as isoclines. While the total SDE of a plant could change if (a) all dispersers respond the same to changing PSM concentrations, it is more likely that (b) PSMs would alter the relative contributions of different dispersers, which may shift in relative effectiveness or community composition (i.e., with some species only dispersing fruits with high or low PSM amounts/diversity).



Box 1. Hypotheses for the Adaptive Significance of Biologically Active Secondary Metabolites in Fruit

Many hypotheses have been proposed to explain the adaptive significance of plant secondary metabolites (PSMs) in fruit in the context of seed dispersal and fruit defense [6,90]. Some hypotheses (e.g., the **attraction/association**, **direct nutritional benefits**, **attraction/repulsion**, and **gut retention time hypotheses**) posit that fruit PSMs evolved to promote seed dispersal by mediating interactions with dispersers. For example, according to the attraction-association hypothesis, fruit PSMs may have evolved to attract dispersers by serving as honest signals that can be associated with rewards. Other hypotheses (e.g., the **directed toxicity** and **defense trade-off hypotheses**) propose that PSMs in fleshy fruits evolved primarily as defense against pre- or post-dispersal seed predators and pathogens. While the directed toxicity hypothesis proposes that PSMs may defend against natural enemies without affecting dispersers, the defense trade-off hypothesis postulates that this may come at the cost of also deterring dispersers.

Many of these hypotheses are non-mutually exclusive, and it is likely that fruit PSMs serve multiple adaptive functions in many cases. However, evidence in support of these hypotheses has been debated, and it is possible that fruit PSMs are not always adaptive in the context of seed dispersal and fruit defense (see Outstanding Questions) [91]. Some compounds may occur due to physiological or phylogenetic constraints or as the result of other selective pressures [26,92,93]. For example, plants may be under strong selection to produce PSMs to defend leaves, and leaf herbivory can induce changes not only in leaf chemistry but also fruit chemistry, with a corresponding reduction in disperser visitation [94]. Fruit PSMs can similarly be influenced by abiotic conditions (e.g., water stress or nutrient limitation), which can also interact with plant genotype and biotic factors [95–98]. Nonetheless, at least in some systems, fruits contain greater concentrations and diversities of PSMs than leaves and roots , and a high proportion of the variance in fruit chemical composition can be explained by frugivore preferences [56,87,98,102,103], suggesting that many compounds likely serve adaptive functions in the context of seed dispersal and fruit defense. Whether or not fruit PSMs are adaptive in mediating seed dispersal, they can have strong ecological effects on interactions with both seed dispersers and pre- and post-dispersal seed predators and pathogens, with important effects on seed dispersal effectiveness and plant fitness.

Box 2. Case Study: Effects of Fruit Secondary Metabolites on Seed Dispersal of *Piper*

Piper (pepper plants) is a diverse genus (>1,000 species) dominant in neotropical forests [104]. Fruits are borne on spike-shaped infructescences and dispersed primarily by bats and secondarily by ants [57]. *Piper* produces a wide diversity of biologically active plant secondary metabolites (PSMs) in all tissues, including unripe and ripe fruit [100,104,105].

PSMs in *Piper* fruits can influence seed dispersal quantity through multiple mechanisms. Volatiles act as primary cues that attract dispersers from a distance (Fig. I) [105,106]. Other PSMs can reduce seed dispersal quantity, including amides and alkenylphenols – two classes of compounds that appear to function primarily in defense but can also reduce the preferences of seed dispersers (Fig. I) [5,7,13]. While amides and alkenylphenols may result in a net decrease in SDE, this may not always be the case. By defending against pre-dispersal fungal pathogens and (for amides) hemipteran seed predators [5,14,100], these compounds could also potentially increase seed dispersal quantity by extending fruit persistence and availability for dispersal.

After fruit removal, PSMs can have multiple contrasting effects on seed dispersal quality of *Piper*. Amides reduce the likelihood of bats consuming fruits, causing them to drop seeds in intact or partially consumed infructescences instead of defecating them in fecal clumps beneath feeding roosts (Fig. I) [7,13]. Amides also reduce the gut retention time of seeds in bats, with corresponding reductions in dispersal distance (Fig. I) [13,68]. Such changes in the quality of seed handling and deposition could alter the likelihood of secondary dispersal, post-dispersal pest attack, and germination [57,78]. For example, seeds deposited in intact fruits (versus fecal clumps) are more rapidly removed by secondary dispersers (Fig. I) [57], which could be advantageous if they deposit seeds in particularly beneficial microsites or clean them with antimicrobial compounds.

PSMs in *Piper* fruit can have both positive and negative effects on different seed dispersal effectiveness (SDE) components, with the potential for trade-offs. Thus, in order to determine their net effects on plant fitness, it is important to evaluate their effects across multiple stages of dispersal. Because the same compounds can be present in multiple *Piper* tissues, understanding their adaptive significance will also require evaluating their effects across multiple life stages (see "Outstanding Questions").

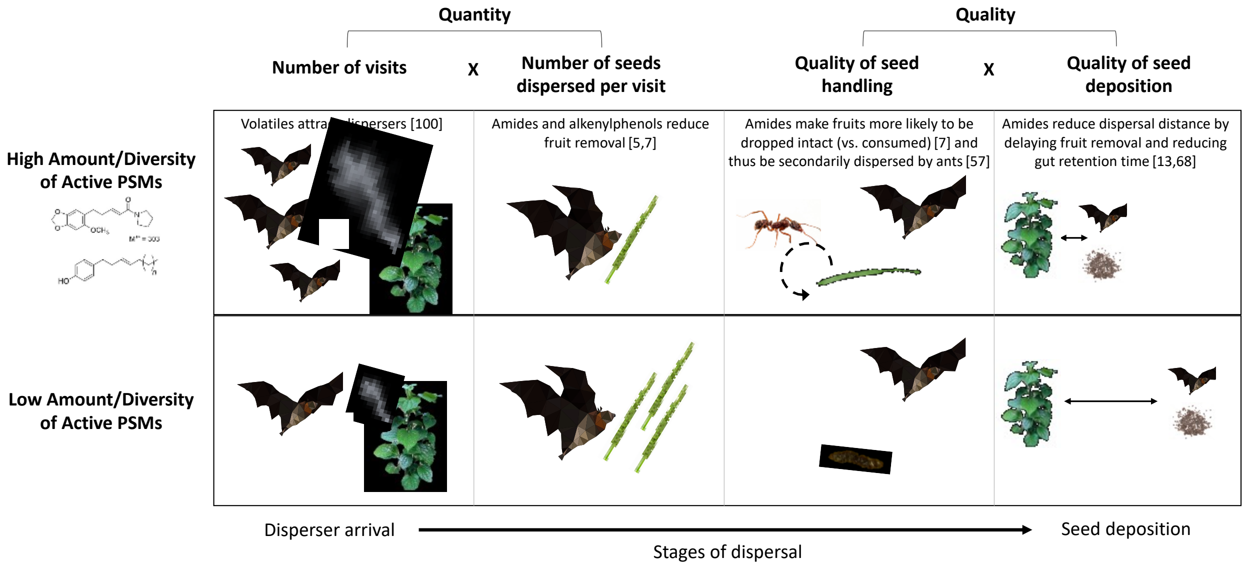


Fig. I. Diagram of the effects of biologically active fruit PSMs on SDE of *Piper*. Known effects of PSMs (at high versus low concentrations), including both attractive volatiles and deterrent amides and alkenylphenols, are shown for all stages of dispersal (from disperser arrival to seed deposition).

Box 3. Outstanding Questions

What are the roles of reliable versus deceptive PSM signals, as well as prior experience and learning by dispersers, in mediating SDE?

How do fruit PSMs alter seed disperser assemblages and the resulting effects on SDE? To this end, further integrating PSMs into fruit-frugivore networks, SDE landscapes, and spatial analyses of seed rain will be helpful.

What are the roles of PSM composition and diversity in mediating SDE? Metabolomics, mass spectrometry, nuclear magnetic resonance, and bioinformatic tools can facilitate the characterization of complex mixtures of secondary metabolites. Recent theoretical advances in applying concepts from the species diversity literature to the study of chemical diversity will allow for descriptions of multiple aspects of chemical diversity (e.g., richness and alpha, beta, and gamma diversity) that can be linked to SDE components.

How do fruit PSMs interact with other plant traits to determine SDE? Many other traits (e.g., plant height, crop size, fruit size, morphology, and nutritional content) also influence SDE, but their relative importance and interactive effects are not well understood.

What is the adaptive significance of different classes of PSMs in fruit, and how do interactions with frugivores shape their evolution and expression? Multiple approaches, such as phylogenetic comparative methods and studies that measure selection on chemical traits by multiple biotic and abiotic agents and across plant tissues, can tackle these questions.

What are the net quantitative effects of fruit PSMs on SDE and plant fitness? Most studies have focused on PSM effects on one or several components of SDE, but the same compounds can have multiple functions, with the potential for trade-offs. Answering this question will require detailed long-term studies in model systems that quantify the effects of PSMs on all SDE subcomponents.

Glossary

Attraction/association hypothesis – Fruit secondary metabolites may provide reliable foraging cues that can be associated with rewards for dispersers [6]

Attraction/repulsion hypothesis – After primary nutrients attract dispersers, secondary metabolites can induce them to leave, which may be adaptive in preventing excessive removal by a single disperser or increasing seed dispersal distance [6]

Defense trade-off hypothesis – Secondary metabolites that deter invertebrate or microbial pests from fruits may also deter effective seed dispersers [6]

Directed dispersal – Seed deposition to particularly favorable microsites, resulting in increased seed dispersal effectiveness

Direct nutritional benefits hypothesis – Fruit secondary metabolites may provide direct nutritional benefits to seed dispersers [90]

Directed toxicity hypothesis – Fruit secondary metabolites may deter vertebrate seed predators but have no effect on dispersers [6]

Frugivore – Any animal that consumes fruit, with either positive (for seed dispersers) or negative effects (for seed predators) on the outcome of seed dispersal

Gut retention time hypothesis – Fruit secondary metabolites may influence gut retention time of dispersers, with effects on the quality of seed handling and deposition [6]

Plant secondary metabolite (a.k.a. “specialized metabolite”) – Although the distinction between primary and secondary metabolites can often be ambiguous, here we define secondary metabolites as any volatile or non-volatile compound produced by a plant that functions primarily in mediating plant-environment interactions, rather than in directly modulating plant growth or metabolism

Secondary seed dispersal – The second stage of seed dispersal which, when it occurs, is often over relatively short distances by animals such as invertebrates or rodents

Seed dispersal effectiveness – The number of new adults a plant produces through the activities of a seed disperser, determined by seed dispersal quantity x quality

Seed dispersal effectiveness landscape – Two-dimensional representations of different possible combinations of seed dispersal quantity and quality across biotic or abiotic contexts

Seed dispersal quality – The net probability that a dispersed seed will survive to produce a new adult, determined by the quality of seed handling x the quality of seed deposition

Seed dispersal quantity – The total number of seeds dispersed, determined by the number of visits x number of seeds dispersed per visit

Seed disperser – Any animal that provides seed dispersal services to a plant, increasing its seed dispersal effectiveness

Seed predator or pathogen – Any organism that attacks seeds, either before or after dispersal, decreasing their probability of survival

Quality of seed deposition – The location and conditions in which seeds are deposited, such as the dispersal distance and deposition microsite, which may determine whether a seed germinates and survives to produce a new adult

Quality of seed handling – The timing and form of seed handling by a disperser, such as whether and when a seed is carried, consumed, and subsequently dropped, spit out, regurgitated, or defecated, which may determine whether it survives dispersal