Evolutionary ecology of pungency in wild chilies


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The primary function of fruit is to attract animals that disperse viable seeds, but the nutritional rewards that attract beneficial consumers also attract consumers that kill seeds instead of dispersing them. Many of these unwanted consumers are microbes, and microbial defense is commonly invoked to explain the bitter, distasteful, occasionally toxic chemicals found in many ripe fruits. This explanation has been criticized, however, due to a lack of evidence that microbial consumers influence fruit chemistry in wild populations. In the present study, we use wild chilies to show that chemical defense of ripe fruit reflects variation in the risk of microbial attack. Capsaicinoids are the chemicals responsible for the well known pungency of chili fruits. *Capsicum chacoense* is naturally polymorphic for the production of capsaicinoids and displays geographic variation in the proportion of individual plants in a population that produce capsaicinoids. We show that this variation is directly linked to variation in the damage caused by a fungal pathogen of chili seeds. We find that *Fusarium* fungus is the primary cause of predispersal seed mortality, and we experimentally demonstrate that capsaicinoids protect chili seeds from *Fusarium*. Further, foraging by hemipteran insects facilitates the entry of *Fusarium* into fruits, and we show that variation in hemipteran foraging pressure among chili populations predicts the proportion of plants in a population producing capsaicinoids. These results suggest that the pungency in chilies may be an adaptive response to selection by a microbial pathogen, supporting the influence of microbial consumers on fruit chemistry.

Capsicum chacoense

T he evolution of fruit, a reward for animal dispersal of seeds, is a commonly cited example of a key innovation in the radiation of angiosperms (1–3). However, the nutritional qualities of fruit pulp that are responsible for attracting beneficial dispersers also attract consumers that are detrimental to plant fitness. These consumers range from vertebrate and invertebrate seed predators to microbial consumers of fruits and seeds that reduce the likelihood of dispersal and the viability of seeds (4). Fruit chemistry is commonly thought to mediate these interactions, either by deterring seed predators (4–6) or reducing microbial attack of fruits and seeds (4, 7, 8). These mechanisms are not mutually exclusive, but chemicals that deter fruit consumption often affect a wide range of species (7, 9), and defensive chemistry in ripe fruit must be sufficiently targeted toward detrimental organisms to allow consumption by vertebrate seed dispersers. Fruit secondary compounds that deter microbial consumers without reducing seed dispersal by vertebrates are thought to be far more plausible than secondary compounds that selectively deter vertebrate predators (7), because microbial fruit consumers are uniformly negative in their impacts on plant fitness (4) and are farther removed in their morphology, physiology, and mode of consumption from vertebrate seed dispersers than are other unwanted consumers (4, 7).

Microbial deterrence is thus a primary hypothesis explaining the presence of noxious, bitter, and sometimes toxic chemicals in many ripe fruits; the negative effects these chemicals often have on vertebrate dispersers are assumed to be balanced by the benefits of deterring microbial consumers. Unfortunately, this hypothesis remains largely untested, because no work to date has shown that variance in microbial pathogen pressure is related to variance in the chemistry of ripe fruits in wild populations. A strong test would require a species in which fruit chemistry is well known, likely to protect against microbial pathogens, unique to the fruit, and highly variable. The most famous plants with these qualities are chilies (genus *Capsicum*). Chilies were one of the first plants domesticated in the New World (10), and they are now consumed by one in four humans daily (11), largely because of the pungency produced by capsaicinoids. Capsaicinoids are well characterized (9) and broadly antimicrobial (12–14). In fact, early humans likely selected chilies for use and domestication expressly because of their antimicrobial properties (12, 15). Finally, because capsaicinoids are found only within the fruit of *Capsicum* species and their concentrations increase during fruit ripening (16), the function of these chemicals is likely restricted in the fruit itself, not attributable to alternative functions in other parts of the plant (17).

Chilies thus provide an exceptionally clear window into the function of fruit chemistry, and our recent rediscovery of a polymorphism for capsaicinoid production in wild populations of multiple chili species (18) provides the variability we need to explicitly examine the function of these chemicals in wild populations. We have studied this polymorphism most intensively in *Capsicum chacoense* Hunz., which is native to the Chaco region of Bolivia, Argentina, and Paraguay (19). In polymorphic populations, *C. chacoense* plants producing fruits that contain capsaicinoids grow alongside plants with fruits that are nutritionally similar (20) but completely lack capsaicinoids (18) (see supporting information (SI)). In addition, the proportion of plants producing capsaicinoids varies widely among populations. At the southwestern end of our 300-km-long study area in southeastern Bolivia, the polymorphism is virtually absent; most populations contain only pungent plants. To the north and east of this area, nonpungent plants gradually increase in frequency, until >70% of individuals lack capsaicinoids, and the few plants that do produce pungent fruit have capsaicinoid concentrations barely one-third the level found in completely pungent populations (18).

We use this geographic gradient as a tool to study the impact of microbial pathogens on fruit chemistry, and we make the following predictions: (i) Microbial fruit pathogens will have a large negative impact on nonpungent chilies, (ii) capsaicinoids will reduce microbial damage to chili fruits and seeds, and (iii) among populations, the proportion of plants producing capsaicinoids will increase as the intensity of microbial attack increases.


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Abstract

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Fruit chemistry is commonly thought to mediate these interactions, either by deterring seed predators (4–6) or reducing microbial attack of fruits and seeds (4, 7, 8). These mechanisms are not mutually exclusive, but chemicals that deter fruit consumption and defend toward vertebrate fruit predators are usually different than those that deter det pungent populations (18). In addition, the proportion of plants producing capsaicinoids vary very widely among populations. At the southwestern end of our 300-km-long study area in southeastern Bolivia, the polymorphism is virtually absent; most populations contain only pungent plants. To the north and east of this area, nonpungent plants gradually increase in frequency, until >70% of individuals lack capsaicinoids, and the few plants that do produce pungent fruit have capsaicinoid concentrations barely one-third the level found in completely pungent populations (18).

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Die beiden Schlusssätze runden die Beschreibung der Eigenheiten mit noch detaillierteren Informationen ab. Diese Sätze untermauern den in der "Topic sentence" geäusserten "Claim" (Behauptung) und beschliessen somit den Abschnitt.

The Einleitungssatz entspricht der Hauptaussage des Abschnitts: Der Polymorphismus von Chilis weist die notwendige Variabilität auf, um die Hypothese zu prüfen. Dabei handelt es sich um den Gedanken, der in den folgenden Sätzen genauer erläutert wird.

Das Wort „thus“ (daher) verweist auf die Aussage des vorhergehenden Abschnitts und lässt eine logische Verknüpfung – und einen schönen Übergang – zwischen den beiden Abschnitten entstehen.