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Community ecology

Sodium-enriched floral nectar increases pollinator visitation rate and diversity

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Plants have evolved a variety of approaches to attract pollinators, including enriching their nectar with essential nutrients. Because sodium is an essential nutrient for pollinators, and sodium concentration in nectar can vary both within and among species, we explored whether experimentally enriching floral nectar with sodium in five plant species would influence pollinator visitation and diversity. We found that the number of visits by pollinators increased on plants with sodium-enriched nectar, regardless of plant species, relative to plants receiving control nectar. Similarly, the number of species visiting plants with sodium-enriched nectar was twice that of controls. Our findings suggest that sodium in floral nectar may play an important but unappreciated role in the ecology and evolution of plant–pollinator mutualisms.

1. Introduction

Many plants increase the quality or quantity of rewards in pollen or nectar to encourage visitation by pollinators [1–3]. Many studies have explored how concentrations of sugars and amino acids in nectar might fuel pollinators and enhance pollination [4–6], but few have explored how many of the other constituents (such as macro- and micronutrients) in nectar may influence both the number and diversity of floral visitors [7–9]. This dearth of studies is surprising because even the minor constituents in pollen and nectar may be adaptive [11]. Here, we explore whether sodium—an important micronutrient [12]—in flower nectar could act to attract pollinators and increase plant visitation.

Why sodium? Ranchers and hunters have long observed that sodium (Na)-enrichment, via salt licks, attracts the large herbivores they are most interested in, for example, cattle, sheep, deer and elk. Indeed, evidence of Na-limitation in nature continues to accrue [12]. Almost 50 years ago, Arms *et al.* [13] documented that Swallowtail butterflies were seeking Na when they puddled. More recently, a number of studies indicate that insect herbivores and detritivores are also attracted to Na: experimentally enriching plots with Na increases the abundance of insect herbivores [14], termite abundance and activity [15,16] and leafcutter ant herbivory [17]. Herbivores in diverse ecosystems selectively browse plants with higher Na content in their leaves [18,19]. If Na attracts herbivores and detritivores, it may also serve to attract pollinators. The limited available evidence illustrates that Na in floral nectar varies substantially

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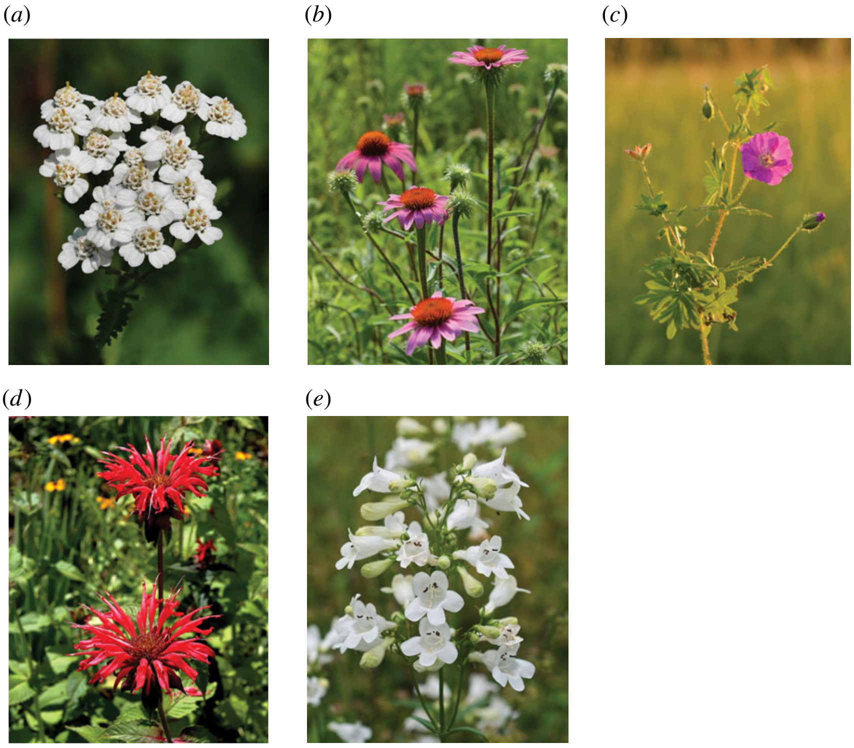

Figure 1. The five focal plant species used in our experiment investigating the influence of sodium-enriched nectar on plant–pollinator interactions: (*a*) *Achillea millefolium* (Asteraceae), (*b*) *Echinacea purpurea* (Asteraceae), (*c*) *Geranium sanguineum* (Geraniaceae), (*d*) *Monarda didyma* (Lamiaceae) and (*e*) *Penstemon digitalis* (Plantaginaceae). Photo credits: (*a*) Petar Milošević, (*b,e*) Eric Hunt, (*c*) Ivar Leidus and (*d*) Burkhard Mücke; all photographs are the photographers' own work and have been made available under Creative Commons licenses CC BY-SA 4.0 (*a,b,d,e*) and CC BY-SA 3.0 (*c*) (https://creativecommons.org/licenses/by-sa).

across species, time and space [8,20]—yet the influence of Na in floral nectar on plant–pollinator interactions has rarely been explored.

Here, we experimentally enriched floral nectar with Na in five plant species in a field experiment to ask whether pollinator visitation rate and pollinator diversity are higher in plants with more Na in their nectar.

2. Material and methods

We conducted this work in a meadow at the University of Vermont's Aiken Forestry Sciences Laboratory in South Burlington, Vermont (elevation: 60 m; 44°27′09.0″ N 73°11′26.7″ W). Common flowering species at the site include *Achillea millefolium*, *Solidago canadensis* and *Asclepias syriaca*. Common pollinators at the site include *Bombus impatiens*, *Bombus vagans* and *Phyciodes tharos*.

We conducted our field experiment using five common plant species in meadows of New England: *A. millefolium* (Asteraceae), *Echinacea purpurea* (Asteraceae), *Geranium sanguineum* (Geraniaceae), *Monarda didyma* (Lamiaceae) and *Penstemon digitalis* (Plantaginaceae) (figure 1). We obtained these plants from two local greenhouses early in the growing season and maintained at least 12 individuals of each species in 23 cm diameter pots in a greenhouse at the site. Plants were kept in a greenhouse, watered twice a day and were not treated with fertilizer.

We experimentally manipulated Na content in half of the plants to examine the influence of Na-enriched nectar on plant–pollinator interactions. We used two stock solutions of artificial nectar: control nectar, which was made up of 35% sucrose (weight : volume), and Na-enriched nectar, which was made up of 35% sucrose + 1% Na (weight : volume) (following [21,22]). We applied 15 µl of our artificial nectar 30 min before each pollinator observation period (at approximately 07.30, 11.30 and 15.30) by inserting the tip of a micro-pipette between the ovary and the stamens of each flower. Plants were in bloom for the duration of the experiment. Pipette tips were changed between each plant to avoid accidental cross-pollination or accidental application of Na to control flowers [23].

Prior to our pollinator observations each day (see details below), we selected six individual plants from each of our focal species, half of which received Na-enriched nectar and the other half received control nectar. We applied artificial nectar treatments randomly to individual plants. We then randomly placed the plants (in their pots) along six 15 m transects. Transects were approximately 3 m from one another. Plants that were designated as Na-enriched received the experimental solution exclusively for the duration of the experiment.

We recorded pollinator visits to flowers from 9 July 2019 to 2 August 2019 on warm, sunny days (no rainfall, ambient temperature greater than 8°C) during three 1 h observation periods beginning at 08.00, 12.00 and 16.00. We recorded the identity and number of each pollinator visiting the flowers of each species across all 30 plants. After each observation period, we walked each of the six 15 m transects for 10 min each and netted visitors on the focal plant species to estimate diversity of floral visitors. If we were unable to identify a floral visitor in the field, we collected it and stored it in 75% ethanol. We identified each pollinator to species or the finest taxonomic level possible.

To ascertain whether Na-enriched plants were visited more frequently by pollinators, we calculated the total number of visitors across all observation periods and days for each individual plant for each species in each treatment. Each individual plant in each treatment was observed, on average, 24 times over the course of the experiment, and each focal plant species was observed, on average, 270 times over the course of the experiment. Because these data are count-based and over-dispersed, we examined differences in the number of visitors between treatments and plant species using a generalized linear model with a negative binomial error distribution. Our model included the number of visitors as the response variable, treatment and

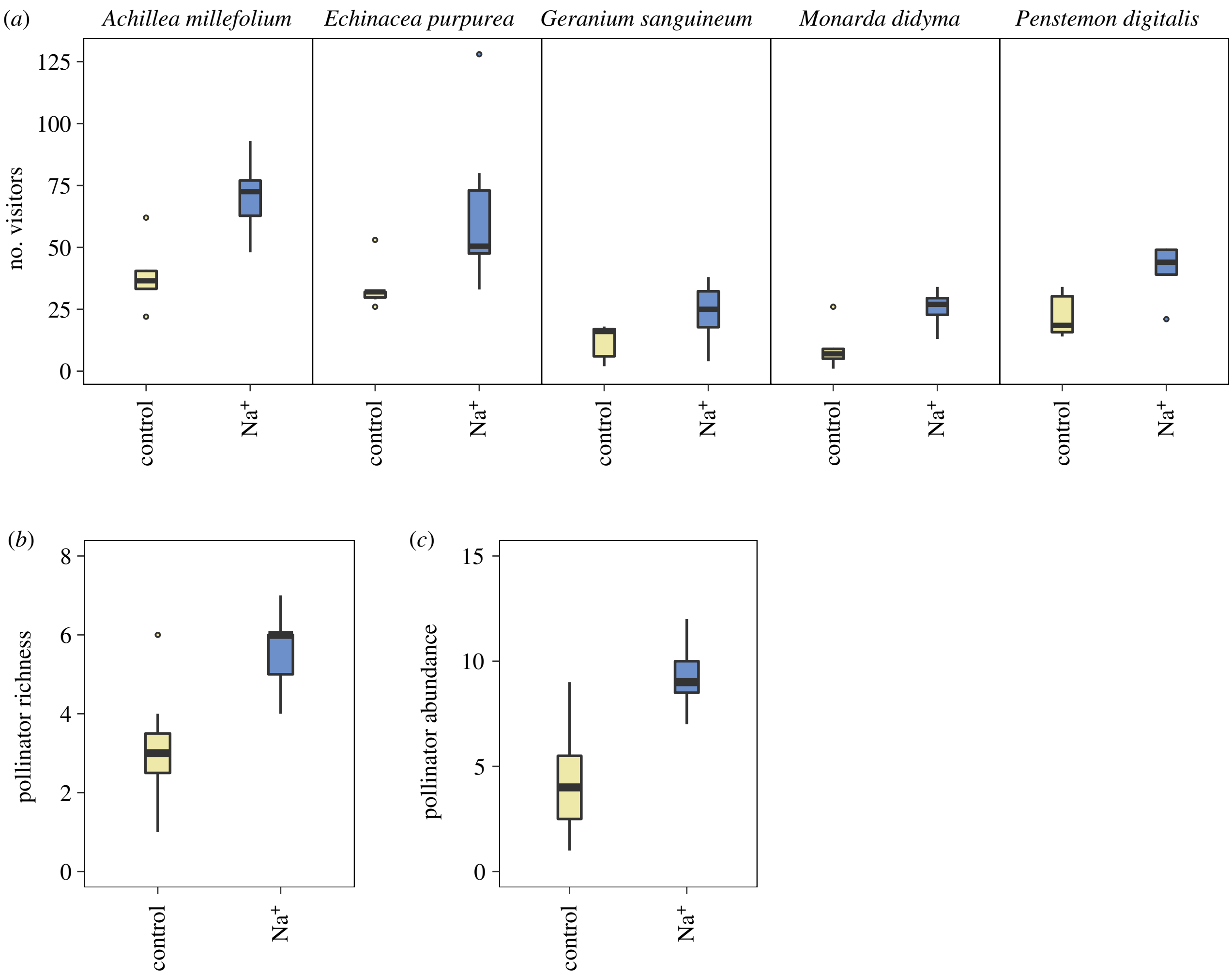

Figure 2. The effect of Na-enrichment on visitation across five plant species in a meadow in Vermont. (*a*) The number of visitors is always greater on Na-enriched flowers, regardless of plant species. (*b*) Species richness and (*c*) abundance of pollinators is higher on Na-enriched plants across all species.

plant species as predictor variables, and a treatment × plant species interaction. We also examined whether plants receiving Na-enriched nectar received a greater richness of pollinators visiting their flowers. For this analysis, we treated each observation day as a sample ($n = 7$) and summed the total richness of pollinators across all plant species within each treatment. Because richness data are count-based, we examined differences in richness between treatments using a generalized linear model with a Poisson error distribution.

All analyses were performed in R (v. 4.0.2) [23].

3. Results

We recorded a total of 1929 pollinator visits to flowers of the five plant species. The most common flower visitors were bees in the Apidae (mostly *Apis mellifera* and *Bombus* spp.), Halictidae (mostly *Augochlora* spp.) and Megachilidae, followed by flies in the Syrphidae, and butterflies in the Nymphalidae (see electronic supplementary material, appendix 1 for more details).

Across all species, there were nearly twice as many visitors on plants with Na-enriched nectar (44.9 ± 5.3 s.e.) than on control plants (24.1 ± 2.8 s.e.). The effect of Na-enrichment was consistent across all five plant species. That is, there was not a significant Na-enrichment × plant species interaction ($F_4 = 0.24$, $p = 0.9224$), indicating that Na-enriched nectar increased visitation by pollinators, regardless of plant species ($F_1 = 22.82$, $p < 0.0001$; figure 2*a*). Overall visitation rates varied among plant species ($F_4 = 12.26$, $p < 0.0001$). *Achillea millefolium* (mean: 54.1 ± 6.3 s.e.) and *E. purpurea* (mean: 49.4 ± 8.4 s.e.) received the most visits, followed by *P. digitalis* (mean: 30.5 ± 4.1 s.e.), *G. sanguineum* (mean: 16.6 ± 3.5 s.e.) and *M. didyma* (mean: 16.6 ± 4.0 s.e.). Finally, species richness of floral visitors was almost 2× higher for plants with Na-enriched nectar than for control plants ($F_{1,12} = 9.42$, $p = 0.0097$; figure 2*b*) and tracked abundance (figure 2*c*).

4. Discussion

Floral nectar evolved as a reward to entice visitors to transport pollen from plant to plant. The general chemical composition of nectar is well-trodden ground [5,24] Most studies agree that potential pollinators are seeking carbohydrates and amino acids in the nectar [25]. Those same pollinators, however, may also be seeking sodium (Na). Here, we show that experimentally Na-enriched nectar across five native plant species increases visitation rate from a diversity of pollinators. Across our five study species, which differed in floral morphology and nectar quality, plants with Na-spiked nectar had nearly twice as many visits by pollinators and nearly twice as many species.

Sodium-limited consumers are attracted to sodium-enriched resources [11]. Swallowtail butterflies 'puddle' [12], some stingless bees drink human tears [26], others seek sodium in carrion [27], sweat bees obtain sodium by licking humans and cattle [28] and water-foraging European honeybees are attracted to sodium-enriched water [29,30]. So perhaps it is not surprising that we found that a suite of pollinators were more attracted to plants with Na-enriched nectar compared with plants without Na-enriched nectar. But why are pollinators attracted to sodium-enriched nectar? Earlier work postulated that pollinators may seek out nectar enriched with NaCl, either because they are seeking only NaCl or because they are seeking NaCl in combination with the amino acid gamma-aminobutyric acid (GABA). GABA plays an important role in neurotransmission, but it depends on sufficient sodium and chloride availability to the organism [31]. Further experiments could distinguish between these possibilities.

Is there any evidence that plants naturally enhance their nectar to compete for or attract pollinators? Na concentration in floral nectar varies considerably among plant species within communities, and even within the same species between seasons and years. For instance, Na concentrations in nectar varied eight-fold among plant species in a montane meadow in Arizona [8], 24-fold in a montane meadow in Colorado [8] and 14-fold in and around Cape Town, South Africa [20]. Whether or not such variation in Na concentration in floral nectar is ecologically meaningful and acts to attract both more and more diverse Na-limited pollinators in nature remains an open question, but our experimental results suggest there is strong potential.

In addition to the increased visitation by pollinators to Na-enriched plants, we also found that Na-enriched nectar attracted a higher diversity of pollinators regardless of plant species identity. Undoubtedly, some of the floral visitors are more effective pollinators than others, and their effectiveness likely varies among plant species. However, there are clear benefits of attracting a diversity of pollinators. For example, the biodiversity insurance hypothesis posits that biodiversity buffers ecosystem functions and services, such as pollination, against the loss of individual species [32–34]. In the case of pollinators, the biodiversity insurance hypothesis predicts that pollinator diversity could increase pollination by increasing the mean, and reducing the variance, of fruit and/or seed set [35] because of complementary pollination among species [36,37], facilitation [38,39] or sampling effects [40]. If most insect pollinators are limited by Na, Na-enriched nectar would be a way to attract more, and more diverse pollinators. In our case, Na-enriched nectar did not attract a suite of species that would otherwise not be attracted to these species. Instead, we observed an increase in biodiversity simply because of a sampling effect: more individuals visited Na-enriched plants, and as a result, there were more species.

The role of sodium and other micronutrients as drivers of ecological processes is only beginning to be explored [11,18,41,42]. Our work suggests that Na could be an important driver of plant–pollinator interactions. Future studies should examine the effectiveness of the pollinators that were attracted to the plants with Na-enriched nectar and to ask whether Na-enriched nectar increases plant fitness. Our work suggests that if plants can increase Na concentrations in nectar, they may be able to better attract Na-limited pollinators, which should ultimately benefit those individuals. Whether sodium-enriched nectar leads to increased fitness of both partners is an open, but testable hypothesis. Moreover, ongoing climate change is expected to alter broad-scale patterns of sodium availability via changes in precipitation and evapotranspiration [43]. Such changes in terrestrial ecosystems will likely have large impacts on the structure and dynamics of plant populations and communities, including how they interact with their enemies and mutualists.

Data accessibility. Data used in this study are available in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.nk98sf7vn [45].

Authors' contributions. C.J.F.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; A.G.: methodology, resources, writing—review and editing; E.A.R.W.: conceptualization, methodology, visualization, writing—review and editing; P.J.C.: formal analysis, visualization, writing—review and editing; M.K.: conceptualization, funding acquisition, writing—review and editing; N.J.S.: conceptualization, data curation, formal analysis, funding acquisition, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Competing interests. We declare we have no competing interests.

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