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# Mechanistic and scale-specific analyses advance the preference–performance hypothesis

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## Abstract

Oviposition choice and larval performance are essential determinants of fitness in plant–herbivore interactions. The long-standing preference–performance hypothesis (PPH) predicts that parents should oviposit on plants that maximize offspring performance; an abundance of work supports the PPH, but many exceptions limit its generality. These exceptions may stem from applying the PPH across diverse contexts without adequately considering mechanistic processes and scale-specific factors. Using the specialist seed predator moth *Schinia florida* and the common evening primrose *Oenothera biennis*, we investigated the mechanistic drivers of preference and performance and how these dynamics shift across scales, between versus within plants. We measured a suite of 126 plant traits, most of which were plant specialized metabolites captured by ultrahigh-performance liquid chromatography and mass spectrometry and applied a novel machine learning approach to identify traits that predict both preference and performance. Between plants, we found no relationship between maternal oviposition preference and offspring performance. Nevertheless, nine overlapping plant traits independently predicted both preference and performance, with all traits positively correlated with preference showing a negative association with performance. This negative trait-based preference–performance link may result from trade-offs of moths using plant defenses as host-finding cues. Overall, weak correlations between the nine predictive traits appear to limit a link between preference and performance between plants. Within plants, moths disproportionately oviposited on flower buds over fruits and concordantly showed higher relative performance on buds. At this scale, only one overlapping trait predicted both preference and performance, and had positive associations with preference and performance. Thus, our results show that (1) a specialist herbivore faces trait-based trade-offs between host selection among plants and larval performance, while making more adaptive decisions at finer scales within plants, and (2) mechanistic and cross-scale approaches offer insight into when adult preference predicts larval performance.


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**KEYWORDS**
chemical ecology, ecological scale, host selection, *Oenothera*, plant–insect interactions, preference–performance relationships, random forest

## INTRODUCTION

Fitness outcomes for herbivores in plant–insect interactions are determined by host preference, especially oviposition choice, and aspects of plant quality leading to variability in larval performance (Awmack & Leather, 2002). The preference–performance hypothesis (PPH) posits that herbivores should prefer to oviposit on plant species on which their offspring have the highest performance (Gripenberg et al., 2010; Jaenike, 1978; Levins & MacArthur, 1969; Thompson & Pellmyr, 1991). At its core, the PPH is an extension of the classic Darwinian notion that organisms should make choices which maximize their fitness, and yet the PPH has received variable support. An early meta-analysis on 110 insect species found support in only 55% of cases (Mayhew, 1997). As with most early work on the PPH, this meta-analysis only considered insect preference between plant species. The PPH has since been extended to include preference for and performance on individuals within a plant species. Gripenberg et al. (2010) found more general support for the hypothesis at both intraspecific and interspecific scales in a meta-analysis of 29 insect species. Still, increasing evidence suggests that preference and performance may function differently when insects are choosing between species versus individuals, or even tissues within a plant (Jones, 2022; Roslin et al., 2006). This scale dependency points to the possibility that the mechanisms driving preference and performance vary across ecological scales.

While the consideration of scale is a more recent development (Jones, 2022), substantial research has been devoted to understanding the cases where the PPH is not supported. These exceptions can be categorized into two main groups: the first comprises deviations that occur due to some constraint that prevents insects from detecting a reliable signal of host plant quality. For example, insects with a wide diet breadth may not be able to perceive plant quality across diverse host species (Craig & Itami, 2008; Gripenberg et al., 2010); alternatively, host plants may change in phenotype (defense, nutritional status, etc.) between herbivore oviposition and offspring maturation leading to unreliable cues (Craig & Itami, 2008). The second set of deviations from the PPH consists of cases where low larval performance in some context trades off with benefits in another context. For example, eggs laid on more toxic plants have been shown to escape predators, parasites, and competitors (Atsatt, 1981; Awmack & Leather, 2002; Björkman et al., 1997; Jones & Agrawal, 2019; Wise & Weinberg, 2002), and toxic compounds can be used by specialists to locate hosts in complex environments (Adler et al., 1995; Ali & Agrawal, 2012; Bruce & Bruce, 2014). While some traits may make herbivores and their hosts more likely to experience constraints or trade-offs that explain exceptions to the PPH, they are not sufficient to predict patterns in adherence to the PPH (Gripenberg et al., 2010). Here, we address two knowledge gaps that help integrate these exceptions into an enhanced framework: (1) is the relationship between preference and performance the same at different ecological scales, and (2) does understanding the mechanisms underlying preference and performance help explain exceptions?

Recent meta-analyses by Jones (2022) and Jones et al. (2019) highlight the importance of scale in the PPH, finding stronger support for the hypothesis when insects choose among individual plants within a species compared to between host plant species. However, despite the potential for ecological scale to impact preference and performance, empirical tests contrasting preference and performance across scales in the same system remain limited. One such study found that the oviposition preferences of *Delia radicum* aligned with the PPH when choosing among *Brassica rapa* cultivars (intraspecific scale) but not across *Brassica* species (interspecific scale) (Menacer et al., 2021). Additionally, adherence to the PPH within individual plants (i.e., between tissues) has been little investigated (Da Silva Galdino et al., 2015; Roslin et al., 2006). Nonetheless, there is tremendous variation within plants (Roslin et al., 2006; Wetzel & Meek, 2019), and several studies indicate that insects feeding on multiple plant tissues exhibit preferences influenced by secondary metabolites, nutritional content, and predators (Kessler & Baldwin, 2002; Smallegange et al., 2007). Indeed, these signals of plant quality are likely scale dependent. For example, *Manduca quinquemaculata* makes oviposition choices between plants based on the presence of competitors, signaled by plant volatiles, while at the smaller within-plant scale, *M. quinquemaculata* bases preference on predation risk (Kessler & Baldwin, 2001, 2002).

While scale can provide a macro-level inference of the ecological factors likely affecting preference and performance, assessing plant traits is a critical mechanistic approach to understand variability in the PPH. Across

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scales, some traits may be consistent predictors of insect behavior, while other traits may have differing relationships with preference and performance. While the role of plant traits, especially defensive traits and other specialized metabolites, has clear importance for preference and performance in plant–insect interactions, very few studies have integrated multiple plant traits in tests of the PPH (see Cornelissen et al., 2008; Gripenberg et al., 2007; Hufnagel et al., 2017; Mason et al., 2019). By assessing how plant traits are correlated with preference and performance (and each other) across scales, we can gain a deeper insight into the scale-specific drivers that help explain variability in the PPH.

Here we seek to advance the PPH by (1) investigating how the preference–performance relationship changes across scales and (2) mechanistically addressing the drivers of preference and performance. For the first objective, we assessed oviposition and larval performance of the primrose moth (*Schinia florida*) between individuals of the common evening primrose, *Oenothera biennis*, and within individual plants (between flower buds and fruits). We hypothesized that at finer scales, the complexity of the environment decreases, allowing for more adaptive oviposition choices, especially for a specialized insect like *S. florida*. To address the second objective, we assessed 126 plant traits, most of which were specialized metabolites measured by ultrahigh-performance liquid chromatography coupled with mass spectrometry, and used novel machine learning approaches to address their predictive ability for preference and performance. Our underlying hypothesis was that the extent to which specific plant traits impact both preference and performance may shape the pattern observed either between or within individual plants.

# METHODS

## Study system

*O. biennis* L. (Onagraceae) is a biennial herb native to eastern North America and is common in open and disturbed habitats. *O. biennis* reproduces mainly through self-pollination, which typically results in genetically identical seeds due to its permanent translocation heterozygote (PTH) genetic system (Cleland, 1972). *O. biennis* has been shown to display genetic variation in multiple defensive traits that influence the local abundance of herbivores, including *S. florida* (Noctuidae), the specialist moth studied here (Johnson & Agrawal, 2007). Past work in this system has also shown that suppression of the insect fauna (including three seed predator moths) results in evolutionary change in plant populations for both reproductive phenology and plant chemical defense (Agrawal et al., 2012, 2021). *S. florida* specializes on *Oenothera* spp. and is also native to eastern North America. Adults oviposit on both the flower buds and fruits of *O. biennis*, after which hatching larvae bore into the tissue they were laid on and consume the reproductive parts, including petals, stamens, stigmas, and seeds (Dickerson & Weiss, 1920; Johnson & Agrawal, 2007).

## Preference–performance experiment

This experiment was carried out on the rooftop patio of Corson Hall at Cornell University in Ithaca, NY (USA). *O. biennis* ($n = 164$ plants) were germinated and grown outside in spring 2012 from the seed of 28 locally collected plants (5–6 replicates per parent plant). There was little to no herbivory. Once plants bolted and were midway through producing buds, flowers, and fruits, we randomized them within a large field cage (4 m × 4 m × 2 m). Twenty-four field-collected adult *S. florida* were released into the cage and allowed to oviposit among the 164 plants for two nights beginning on July 28. To test oviposition preference across scales, we counted the number of eggs laid on buds and fruits of each plant and present the sum (scale 1, between individual plants) as well as the proportion laid on each tissue (scale 2, within individual plants). Because multiple females oviposited simultaneously, preference reflects realized oviposition at the plant or tissue level, which captures the aggregate outcome of individual oviposition decisions across plant phenotypes. Over two nights, *S. florida* females oviposited 151 eggs on 48 plants; 84 of 151 *S. florida* individuals died either as eggs or within the first day of larval development, leaving 67 eggs on 28 plants.

Following the choice experiment, we measured two corresponding metrics of larval performance: larval relative growth rate (RGR) and young larval survival. To control for *S. florida* density in our RGR assays we ensured that each plant had only one surviving larva. Surplus larvae were removed one day after hatching and placed on plants that had not received natural oviposition (67 plants total). This design preserves direct pairing of preference and performance on all oviposited plants, while extending performance measurements to plants with zero oviposition and allowing us to assess a broader range of variation in plant traits. Larvae were placed on the buds of new plants unless that plant had no buds left (in which case they were placed on fruits). Once placed on the new plant, larvae could move between tissues but remained on that individual plant. We weighed these larvae on day 4 and day 6 of development and computed

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RGR of the larvae from this data using the equation RGR = ln(final mass/initial mass)/2. Previous studies have not investigated the PPH within individual plants in part because many insect larvae move between tissue types early in development (Jones, 2022). To address this constraint, we used young larval survival as our performance metric at the within-plant scale. Survival was measured the day after larvae hatched; at this stage, larvae are not mobile and typically remain on the tissue they were laid on, allowing oviposition preference to be matched with performance. We look at both survival and RGR as our performance metric for the between-individual scale because RGR captures a longer period of larval development and is less susceptible to stochasticity than young larval mortality.

## Trait measurements and chemical analyses

To understand the mechanisms governing *S. florida* oviposition choice and larval performance, we measured 126 plant traits including 8 morphological and phenological traits and 118 chemical traits. The nonchemical traits measured include plant phenology (time to first flower), plant height, number of open flowers, number of flower buds, number of fruits, flower bud nonglandular trichome density, flower bud glandular trichome density, and glandular trichome pH. Chemical traits were measured separately in both buds and fruits and treated as distinct traits in our analysis. We used colorimetric assays to measure integrative measures of phenolic activity (such as alkaline oxidative activity) and ultrahigh-performance liquid chromatography diode array detection mass spectrometry (UHPLC–DAD-MS) to measure the main phenolic metabolites of *O. biennis* (ellagitannins, galloyl glucoses, flavonoid glycosides, and caffeic acid derivatives). Many of these metabolites function defensively against *S. florida* and generalist herbivores in *Oenothera*, particularly ellagitannins (e.g., oenothein A) and associated alkaline oxidative activity, which are consistently associated with reduced herbivore preference and performance (Anstett et al., 2019; Johnson et al., 2014). See Appendix S2 for detailed trait measurement methods.

## Statistical analysis

Statistical analysis was performed in RStudio version 4.4.1 (2024-06-14) (R Core Team, 2023). We used a linear model to examine the relationship between preference (total eggs laid per plant) and performance (RGR) between individual plants. Within plants (between flower buds and fruits), we assessed oviposition preference by calculating the ratio of eggs laid on buds to total eggs laid for each plant, expressed as: $\frac{\text{no. eggs laid on buds} - \text{no. eggs laid on fruits}}{\text{total eggs}}$. This metric ranges from −1 (all eggs laid on fruits) to 1 (all eggs laid on buds), with 0 indicating no tissue preference. We then used a quasibinomial generalized linear model (GLM) to assess the relationship between preference (ratio of eggs on buds) and performance (young larval survival), accommodating overdispersion and the bounded nature of the proportion. We additionally quantified the variation in preference and performance structured by genotype using mixed-effects models with genotype as a random factor.

We used machine learning in the form of random forest feature selection with the Boruta wrapper algorithm to find all relevant traits predicting preference and performance (Kursa & Rudnicki, 2010; Liaw & Wiener, 2002). This approach was chosen because of the large number of predictors in our trait data. The Boruta wrapper assesses each trait's importance by comparing it to a randomized "shadow" version of the trait (created by permuting its values); ultimately selecting traits that are more relevant to the independent variables (preference or performance) than their "shadow." This method helps control for false positives and identifies traits whose relationship with preference or performance is unlikely to occur by chance while retaining correlated traits if they are informative. We replicated our random forest approach for preference and performance metrics at the between-plant scale (RGR and total eggs) and the within-plant scale (proportion of eggs on buds and survival). Because the Boruta wrapper does not accommodate random effects, we included plant genotype as a categorical predictor to account for potential nonindependence.

To generate a comprehensive list of relevant predictors, we applied the Boruta random forest algorithm separately to three subsets of our data; see detailed methods in Appendix S2. The random forest algorithm assesses the information content of each trait; however, it does not provide information about the directionality of relationships. To determine the directionality of the selected traits, we used individual linear regression analyses between individual traits and preference and performance. These regressions were used only to assess the sign of the slope as the importance value obtained from the random forest algorithm already provides the most robust estimate of the trait relationship with preference (or performance). Additionally, we evaluated the correlations between traits using Pearson's correlation coefficient and visualized them using the "corrplot" package in r (Wei & Simko, 2021). Because tissue abundance emerged as an important predictor of preference and

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performance, we conducted additional GLM's with offsets to test whether preference scaled proportionally with tissue availability (Appendix S2).

We used principal components analysis (PCA) alongside Boruta random forest to investigate the underlying mechanisms of preference and performance. While random forest was used to identify individual traits predicting preference and performance in our dataset, PCA allowed us to reduce dimensionality. PCA and subsequent principal component regression (PCR) also allowed us to assess the relationship between preference, performance, and combinations of traits rather than signal traits. This analysis of trait combinations may better represent herbivore choice and performance traits (Edwards et al., 2023; Riffell et al., 2009). PCA also served as independent validation of our random forest analysis. Our confidence in the relevance of a trait was increased if it was identified as important by random forest and had a high loading on a principal component that was associated with preference and performance itself. Full details of PCA and PCR analyses are provided in Appendix S2.

## RESULTS

### Pattern and process of the preference–performance relationship between plants

In our mesocosm cages, *S. florida* adults oviposited 151 eggs on 48 of 164 *O. biennis* plants. We found no significant relationship between moth oviposition preference (total eggs laid per plant) and larval performance (RGR) between plants (Figure 1A; $\beta = -0.01$, 95% CI [−0.04, 0.01]). Similarly, young larval mortality was not correlated with oviposition preference ($\beta = 0.15$, 95% CI [−0.03, 0.35]). Genotype explained a moderate proportion of variance in oviposition preference (intraclass correlation coefficient ([ICC] = 0.29), little variance in larval performance (RGR; ICC = 0.02), and did not explain covariance between preference and performance (singular fit; ICC = 0). Despite the apparent lack of correlation at this scale (Figure 1A), random forest analysis of 126 plant traits identified 41 traits that predicted preference and 17 that predicted performance (Appendix S1: Tables S1 and S2). Among these 49 distinct traits, nine overlapped in predicting both preference and performance (Tables 1 and 2). The importance values ($z$-scores) reflecting each trait's contribution to model accuracy for preference and performance were of similar magnitude in overlapping and nonoverlapping traits (preference: mean $z$-score of 4.37 for overlapping traits and 4.55 for nonoverlapping traits [Appendix S1: Table S1]; performance: mean $z$-score of 4.12 for overlapping traits and 5.15 for nonoverlapping traits [Appendix S1: Table S2]). In other words, overlapping traits and nonoverlapping traits should have similar influence on insect behavior. While fruit number was one of the overlapping traits, egg deposition on fruits was less than proportional to fruit abundance ($\alpha = -5.49$, 95% CI [−6.03, −5.02]).

Remarkably, all nine overlapping traits had opposing associations with preference and performance: Seven were positively correlated with preference and negatively correlated with performance, while two exhibited the

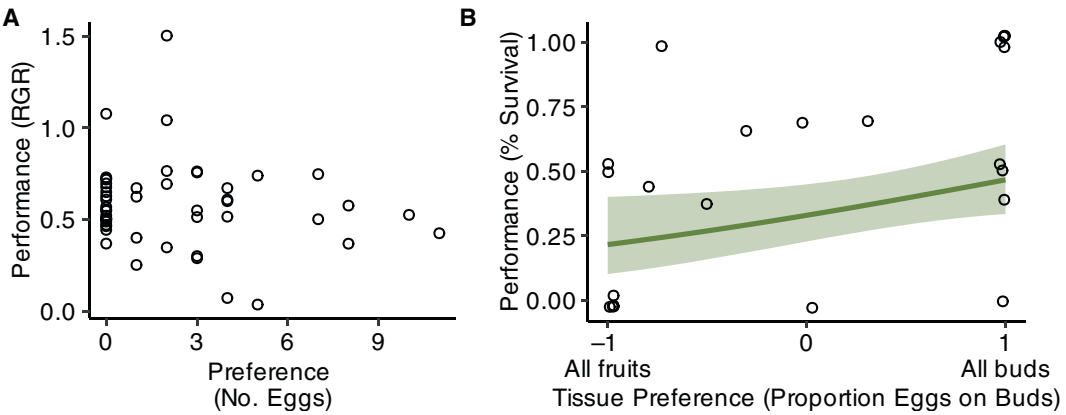


**FIGURE 1** Preference versus performance of *Schinia florida* moths on *Oenothera biennis* (A) between plants, and (B) within plants. (A) Preference refers to the number of eggs laid on individual plants. Performance refers to the relative growth rate (RGR) of *S. florida* larvae on a single plant, excluding mortality. Points represent *O. biennis* individuals. There is no overall relationship between preference and performance. (B) Tissue preference refers to the proportion of eggs laid on buds of *O. biennis* by *S. florida* adults, calculated as (eggs on buds − eggs on fruits)/total eggs. Values of 1 indicate all eggs were laid on buds for that plant, −1 indicates all eggs were laid on fruits, and 0 indicates no tissue preference. Performance refers to the proportion survival of all larvae on that same plant. Due to a large overlap of points, individual datapoints are jittered; the green line shows a quasibinomial regression with 95% CI. Across all plants, females laid 27% more eggs on buds than on fruits.

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**TABLE 1** Traits from our random forest feature selection that predict both moth preference and performance at the between-plant scale (nine traits).

| | Preference (Oviposition) | | Performance (RGR) | |
|---|---|---|---|---|
| | Importance[a] | Direction | Importance[a] | Direction |
| Total monomeric ellagitannins (bud) | 8.27 | − | 4.20 | + |
| Alkaline oxidative activity (fruit) | 5.95 | + | 2.99 | − |
| Total phenolics by the Folin-Ciocalteu method (fruit) | 4.35 | + | 3.57 | − |
| Total kaempferol glycosides (fruit) | 4.15 | + | 2.70 | − |
| Total oligomeric ellagitannins (fruit) | 4.10 | + | 4.72 | − |
| Plant height | 3.86 | + | 3.68 | − |
| No. fruits | 3.16 | + | 6.67 | − |
| Total trichome density | 3.14 | + | 5.63 | − |
| Coumaroyl quinic acid 2 (fruit) | 2.31 | − | 3.80 | + |

[a]Importance values are *Z*-scores generated by random forest reflecting each trait's contribution to model accuracy for preference and performance. A trait with higher importance is more predictive of preference or performance. Direction indicates positive or negative linear regression slopes with preference or performance.

**TABLE 2** Traits from our random forest feature selection that predict both moth preference and performance at the within-plant scale (one trait).

| | Preference (proportion eggs on buds) | | Performance (survival) | |
|---|---|---|---|---|
| | Importance[a] | Direction | Importance[a] | Direction |
| No. buds | 8.47 | + | 17.19 | + |

[a]Importance values are *Z*-scores generated by random forest reflecting each trait's contribution to model accuracy for preference and performance. Direction indicates positive or negative linear regression slopes with preference or performance.

opposite associations (Tables 1 and 2). Although this result suggests a potential negative preference–performance relationship between plants, the nine traits were weakly correlated: Only 15 of the 36 possible pairwise correlations were significant and the average *r*-value of these 15 was 0.47 (Figure 2). Three correlations were very high ($r > 0.95$) among total phenolics, oxidative activity, and total oligomeric ellagitannins, reflecting their biochemical relatedness. Excluding these, the average *r*-value was 0.35 (Figure 2). Thus, although multiple plant traits jointly impact preference and performance, the multiple traits themselves do not come together to shape a preference–performance relationship among plants.

We next used PCA on 78 noncumulative plant traits (see *Methods*) to address preference and performance in a multivariate framework. We regressed the six retained principal components (PCs) against preference and performance (Appendix S2: Figure S1). Notably, PC2 was significantly negatively correlated with preference (Figure 3A: $\beta = -0.36$; 95% CI [−0.56, −0.18]) and positively correlated with performance (Figure 3B: $\beta = 0.029$; 95% CI [0.004, 0.055]). While PC2 was the only axis correlated with performance, PC4 and PC5 were also correlated with preference (Appendix S2: Tables S1A and S2).

Among the 27 traits identified as important on PC2 (Appendix S2: Table S2), 12 overlap with the 29 noncumulative traits selected as predictors of preference and/or performance using random forest (Appendix S2: Table S2). A majority of the nine predictors common to both preference and performance were cumulative traits and therefore not included in our PCA (Tables 1 and 2), but many of their component traits had high loadings on PC2. Oenothein A and B had high loadings on PC2 (Appendix S2: Table S2) and together comprise 94% of total oligomeric ellagitannins in fruit, which was one of the nine overlapping predictors. Likewise, fruit kaempferol diglycoside/glucuronide and bud pentameric/trimeric tellimagrandin I loaded strongly on PC2 and are respectively captured by fruit total kaempferol glycosides and bud total monomeric ellagitannins (Tables 1 and 2).

## Pattern and process of the preference–performance relationship within plants

We found a positive preference–performance relationship within plants: *S. florida* laid 27% more eggs on buds than

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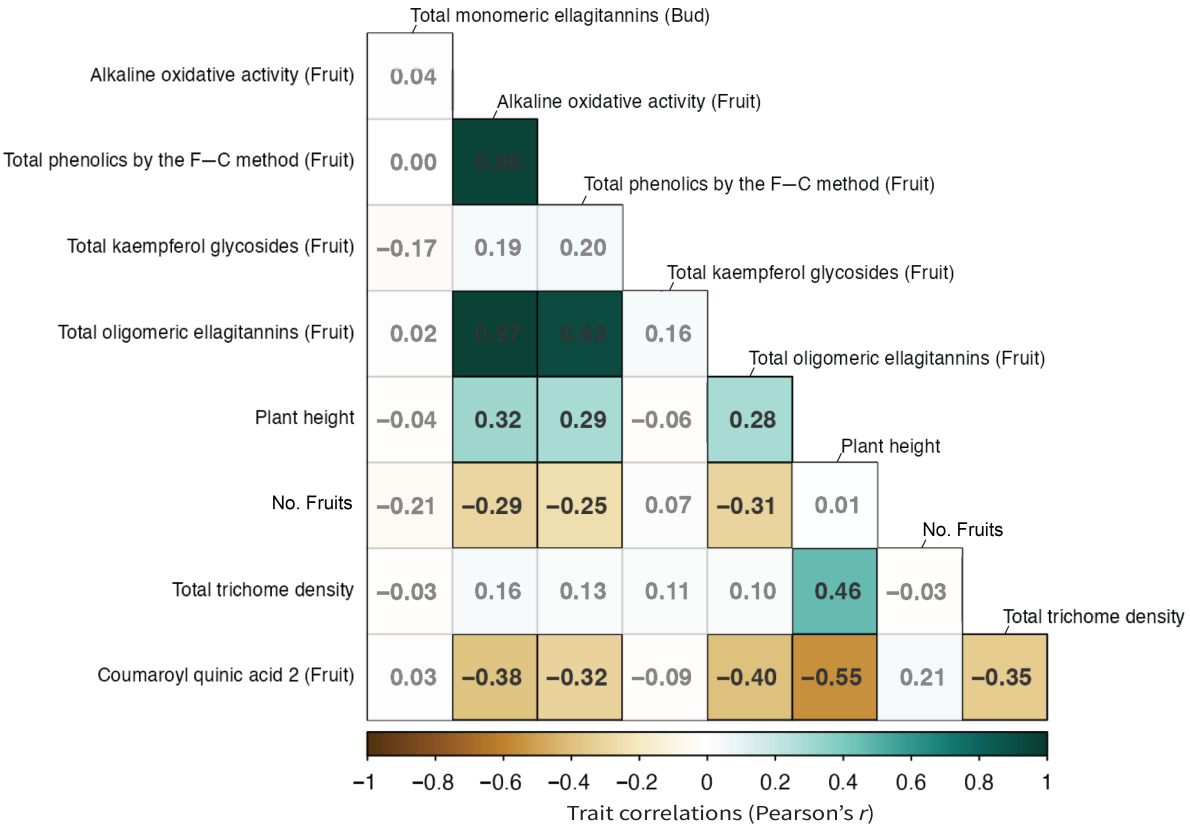


**FIGURE 2** Pairwise correlation matrix for the nine overlapping traits predicting both preference and performance between plants. Only significant correlations ($p < 0.05$) are colored. Correlation coefficients (Pearson's $r$) are shown as black numbers and indicated by the color scale ($n = 76$). F–C method, Folin–Ciocalteu method.

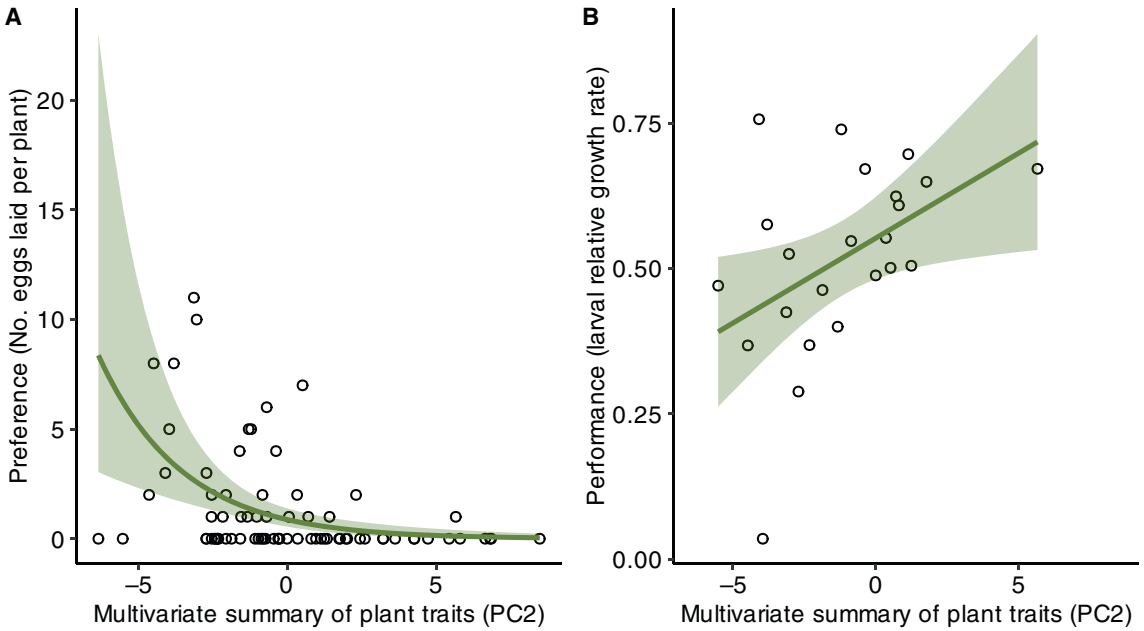


**FIGURE 3** Effect of a multivariate summary of all noncumulative plant traits (principal component 2 [PC2], Appendix S2: Table S2) on (A) preference (number of eggs laid by *Schinia florida* per individual *Oenothera biennis*) ($n = 76$) and (B) larval performance (relative growth rate of *S. florida* larvae) ($n = 23$). The decreased sample size in panel (B) is due to the exclusion of larval mortality. PC2 represents 11.4% of the variance among plants. Points are individual plants. The green line is a negative binomial (A) or linear regression (B) with 95% CI.

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fruits, and this tissue preference was positively correlated with larval performance (survival) (Figure 1B; $\beta = 0.58$, 95% CI [0.06, 1.15]). On average, plants had 57% more fruits than buds (the preferred tissue), with an average of 82 fruits and 22 buds per plant (Appendix S2: Figure S3). We found no relationship between the date of first flower and tissue preference ($\beta = -0.06$, 95% CI [−3.43, 3.32]) or survival (Appendix S2: Figure S4, $\beta = -1.67$, 95% CI [−9.90, 6.56]), suggesting that the preference for buds was driven by tissue-specific qualities rather than plant phenology. Genotype explained a moderate proportion of variance in tissue preference (ICC = 0.19), survival (ICC = 0.16), and in the preference–performance relationship (ICC = 0.14).

Analysis of plant traits among the two tissues within plants supported the positive preference–performance relationship. Random forest revealed fewer predictive traits within plants compared to between plants; of the 126 plant traits, 17 predicted tissue preference and 13 predicted larval survival (Appendix S1: Tables S3 and S4). Among these 29 distinct traits, only one overlapped in predicting both preference and performance: number of buds (Table 2). Notably, preference and performance were both positively correlated with the number of buds (Table 2). Eggs were allocated to buds at a higher rate than expected based on their relative abundance ($\alpha = 2.32$, 95% CI [1.58, 3.11]). Despite these findings, we did not find significant relationships between preference or performance and any of the six retained PC axes in the PCR (Appendix S2: Figure S2, Table S1B).

## DISCUSSION

### Preference–performance relationship between individual plants

While we found no significant correlation between preference and performance on the between-plant scale (Figure 1A), the traits underlying preference and performance suggested a negative relationship (Table 1, Figure 3). Specifically, traits that are attractive (positively predicting preference) lead to lower larval growth rates (negatively predicting performance) (Table 1). Independent statistical analysis of plant chemistry using PCR supported our random forest methods and confirmed a trait-driven inverse relationship between preference and performance (Figure 2). The convergence between traits selected by random forest and traits on PC2 substantiates the importance of the identified traits to preference and performance. The function and importance of the traits identified in our analysis also align with other studies involving *Oenothera* sp. For example, hydrolysable tannins (such as oenothein-type compounds and other ellagitannins) have comparatively high oxidative capacity against caterpillars (Barbehenn et al., 2006). Oenothein A specifically has been shown to be an effective defense against specialist seed predators in *Oenothera* (Agrawal et al., 2012; Anstett et al., 2019).

While the negative relationship between preference and performance indicated by plant traits would appear nonadaptive, we speculate reasons for this relationship based on documented exceptions to PPH. One explanation is that *S. florida* uses certain specialized metabolites of *O. biennis* to locate the plant in a complex landscape, even if these compounds ultimately impair larval growth. This phenomenon has been shown in other specialists like *Junonia coenia*, which uses iridoid glycosides in *Plantago lanceolata* for host finding, despite reduced larval performance on plants with higher iridoid content (Adler et al., 1995). A similar pattern occurs in the cabbage white butterfly (*Pieris rapae*), a specialist which uses glucosinolates as oviposition cues (Huang & Renwick, 1994). Another explanation for this negative relationship is that more highly defended, chemically toxic plants could provide larval refuge from predators (Björkman et al., 1997). In this scenario, the selection of toxic plants would be indirectly beneficial. In our experiment, plants were kept in a cage to exclude predators or competitors; however, we have independently observed *S. florida* larvae being preyed upon by damsel bugs (*Nabidae*). While *S. florida* is not known to sequester plant defense compounds, other traits such as glandular trichomes can create enemy free space for larvae (Atsatt, 1981; Murphy, 2004) and create negative preference performance relationships (Murphy, 2004).

The discrepancy between the absence of a direct correlation between preference and performance among plants and the presence of a negative correlation between the common subset of plant traits predicting preference versus performance may stem from the fact that insects respond to plant hosts based on complex trait combinations rather than single traits (Edwards et al., 2023; Riffell et al., 2009). Traits that predict preference but not performance may provide important context for oviposition stimuli, potentially obscuring the relationship found for our smaller subset of nine overlapping traits (Tables 1 and 2). Additionally, because traits predicting both preference and performance were not highly correlated among plants (Figure 2), individual plants appear to be complex mosaics of important cues. This makes it possible for individual traits to show a negative preference–performance relationship, although this relationship was obscured when preference and performance are averaged across whole plants. Our results are congruent with a study investigating the preference and performance of the specialist stem boring weevil (*Tyloderma foveolatum*) on multiple genotypes of *O. biennis* (Carmona & Johnson, 2016). While it was found

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that common plant traits were predictive of preference and performance, that relationship was not apparent at either scale measured (between individuals or between genotypes). One alternative explanation is that preference may be shaped by density-dependent processes, such as induced plant defenses, which our design would not capture because larval density was standardized (Ellis, 2008).

## Preference–performance relationship within plants

We found a positive preference–performance relationship within plants; *S. florida* preferred to oviposit on flower buds over fruits and their offspring showed concordant enhanced performance on buds (Figure 1B). This positive relationship makes intuitive sense as many of the proposed factors that modify preference–performance relationships (such as competition, predation, and insect perception) are scale dependent (Gripenberg et al., 2007). For example, the need to locate host plants may come at the cost of low larval performance due to attractive defensive compounds (Adler et al., 1995). However, once a host plant is found, moths are free of host-finding constraints and can choose to oviposit on the tissue that maximizes larval performance.

The comparison of mechanistic approaches across scales revealed distinct processes driving preference–performance relationships. Between plants, multiple chemical traits predicted both preference and performance (Table 1), and there were significant correlations between trait combinations from PCR (Figure 3). However, these traits were not predictive of preference and performance at the within-plant scale. Within plants, only one trait, number of buds, influenced both preference and performance (Table 2). Measures of tissue abundance were important at both scales but functioned differently. Between plants, fruit number positively predicted preference and negatively predicted performance (Table 1), and egg allocation did not track fruit availability. In contrast, within plants, bud number positively predicted preference and performance (Table 2), and eggs were allocated to buds at a higher rate than expected based on bud relative abundance. These results suggest that tissue abundance can function as a true signal of tissue quality, though in a scale-dependent manner. Additionally, combinations of traits summarized by PCs did not correlate with preference or performance at the within-plant scale (Appendix S2: Table S1B). This disparity suggests a shift in the relative importance of chemical traits across scales, as multiple chemical cues drive interactions at the between-plant scale but not within plants. Within plants there may be other traits underlying preference and performance that we did not measure such as physical structure and nutritional content (Wetzel et al., 2023). In other systems, toughness and nutrition can have greater effects on herbivores than defensive phenolics, although this has not been explicitly shown in buds and fruits (Cates, 1980).

Despite the potential for ecological scale to impact preference and performance, few empirical tests have assessed the PPH across scales (Menacer et al., 2021). Several studies testing the PPH across scales have found no support for PPH at either scale, yet still find relationships between plant traits and patterns of preference and performance (Gripenberg et al., 2007; Roslin et al., 2006). Congruent to our findings, these studies emphasize the importance of assessing plant traits in understanding preference and performance, and find more support for the PPH at smaller ecological scales (Bergamini & Almeida-Neto, 2015).

## Novel application of Boruta random forest helps find traits underlying the PPH

In recent years, machine learning random forest algorithms have been increasingly employed in ecology to distill meaningful traits from large datasets, particularly in relation to host choice and oviposition preferences (Hopkins et al., 2017). The Boruta wrapper has been adopted by ecologists as it can filter out noise and identify the most important variables from complex ecological datasets (Baleba et al., 2019; Bass et al., 2024). Our study takes a significant step forward by using the Boruta random forest algorithm in a novel way—specifically, we apply it to examine the overlap of trait predictors between two critical ecological variables: oviposition preference and larval performance. This integration allowed us to assess the mechanisms underlying the preference–performance relationship and uncover trade-offs or synergies that the overall preference–performance correlation might obscure. This was the case between plants, where using these methods revealed a negative trait-level relationship between preference and performance (Table 1). This insight enabled us to speculate on specific trade-offs, such as host finding, that may influence the PPH at the between-plant scale. This approach represents a step forward in generalizing the PPH by increasing our mechanistic understanding.

### AUTHOR CONTRIBUTIONS

Scott H. McArt and Anurag A. Agrawal conceptualized and designed the experiments. Scott H. McArt performed the rooftop choice experiment and measurement of morphological traits. Juha-Pekka Salminen measured chemical trait data. Kelley F. Slimon analyzed the data and wrote the initial manuscript, and all authors revised the manuscript.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data and code (Slimon et al., 2025) are available in the Cornell University Library eCommons Repository at https://doi.org/10.7298/n064-ne73.

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