Predictability of bee community composition after floral removals differs by floral trait group

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Plant–bee visitor communities are complex networks. While studies show that deleting nodes alters network topology, predicting these changes in the field remains difficult. Here, a simple trait-based approach is tested for predicting bee community composition following disturbance. I selected six fields with mixed cover of flower species with shallow (open) and deep (tube) nectar access, and removed all flowers or flower heads of species of each trait in different plots paired with controls, then observed bee foraging and composition. I compared the bee community in each manipulated plot with bees on the same flower species in control plots. The bee morphospecies composition in manipulations with only tube flowers remaining was the same as that in the control plots, while the bee morphospecies on only open flowers were dissimilar from those in control plots. However, the proportion of short- and long-tongued bees on focal flowers did not differ between control and manipulated plots for either manipulation. So, bees within some functional groups are more strongly linked to their floral trait partners than others. And, it may be more fruitful to describe expected bee community compositions in terms of relative proportions of relevant ecological traits than species, particularly in species-diverse communities.

1. Introduction

Network analyses are a powerful tool for understanding associations between flowering plants and their visitors. When communities are disturbed, studies frequently assume obligate bee–flower associations, where flower loss causes co-extinction of uniquely associated bees, or vice versa (e.g. effects of invasive plant species [1], simulated species loss [2,3]). Simulations suggest, however, that some networks may be robust to environmental change if visitors can adjust floral partners after disturbances [4–6]. This work has only just begun experimentally [7,8], such as one study where experimental removal of a single bumblebee species increased network connectance and decreased resource complementarity [9].

Functional traits guide species’ environmental responses [10] and partner interactions [11]. Some interactions may be fully ‘forbidden’ by morphological or temporal mismatches [12]. Traits such as bee tongue-length limit possible partners depending on nectar depth [13,14], suggesting flowers may have more or less faithful visitors depending on accessibility. Other ecological factors interact with these traits to shape realized interactions (e.g. nectar quality; relative species abundances [14]; bumblebees experimentally freed from competitors became less faithful to trait-matched flowers [15]).

Flowers in two trait groups with different nectar access depths were experimentally removed from small plots to examine the short-term robustness of bee–flower associations. Bee communities in manipulated plots were compared with communities on the same flowers in controls. Tongue-length was used as
a response trait [13]. I expected bee communities on flowers requiring more specialized visitors to be more predictable after disturbance. That is, I expected long-tongued bees could access all flowers, so would continue to visit plots without tube flowers, while short-tongued bees would avoid manipulated plots where open flowers with shallowly accessible nectar were removed.

### 2. Material and methods

I selected six meadows in Tolland County, CT, USA, with diverse flowers of ‘open’ and ‘tube’ morphology, defined, respectively, as a flat corolla and easily accessible nectar, or nectar hidden at the bottom of a tubular corolla [14]. Species identified using field guides during site selection varied widely among fields (table 1).

In each field, three $3\times6$ m plots were identified with similar...
floral cover, internally and among plots (figure 1a). Half of each of the first two plots was manipulated, one with open flowerheads and the other with tube flowers removed. The other half of each was kept for control. The third, a control, was placed at least 7 m away, in case manipulations caused changes in floral choices in immediately adjacent areas. Only flowers or flowerheads were removed. Manipulations were compared with co-temporal controls rather than before–after (e.g. [7]) owing to rapid temporal turnover in pollinator networks [16].

I observed bee visits in July 2015 within a day of floral manipulation, between 09.00 and 17.00 h on sunny or brightly overcast days over 24°C with low wind. Each plot was observed for an hour, one half-hour per half-plot. The number and species of flowers visited were recorded. Observations, timed with a stopwatch, started when a bee landed on a flower and ended when the bee left the plot. Twenty minutes were added if 16 bees/plot were not seen for at least 30 s each. To allow natural foraging, bees were not captured. Bees were identified to morphospecies groups consistent with other studies using on-the-wing identification [17]: long-tongued (Apidae, Megachilidae): _Apis mellifera_, _Bombus_, _Ceratina_, ‘Megachilid’, _Melissodes_, _Osmia_; short-tongued (Halictidae, Colletidae): ‘green bee’, _Halictus_, _Hylaeus_, _Lasioglossum_ (see Discussion; voucher photos in electronic supplementary material, Methods).

3. Results
I followed 516 bees visiting 3565 flower heads during 482 min, with a per-field average of 87 bees (range 70–114) and 594 flowerheads (range 476–816) and per half-plot average of...
14 bees (simplified interaction networks, figure 1b). In all fields I observed Bombus (272 total bees across all fields), green bees (72), Halictus (52) and Lasioglossum (40); in four fields, A. mellifera (24 bees) (raw data in electronic supplementary material, table S2). Field-level accumulation curves quickly plateaued for fields and manipulations, suggesting well-sampled morphospecies (electronic supplementary material, figure S1).

With open flowers removed, the remaining bee community was not different from bees on the tube flowers in controls (figure 2a, light-grey boxes; electronic supplementary material, table S1); floral loss did not change floral choice. But with tube flowers removed, bees on remaining open flowers were dissimilar from bees on open flowers in controls (figure 2a, dark-grey; electronic supplementary material, table S1). The bee community that visited open flowers was more diverse than that for tube flower visitors (electronic supplementary material, figure S2; conceptual summary figure 2c).

In the first GLMM, long-tongued bees were a significantly different proportion of the community in each manipulation compared with controls (table 2). In the second GLMM, confidence intervals of observed and predicted proportions of long-tongued bees overlapped (table 2: least-square means, model 2). Thus, the measured proportion of short- and long-tongued bees was not different from the predicted proportion. But, a significant interaction between the manipulation and observed status (table 2) indicates that each bee trait group was slightly less faithful to their floral partners in manipulations than controls (figure 2b).

4. Discussion

Given high bee diversity [5], accurately predicting species composition following disturbance will always be a challenge. But, this study accurately predicted the relative proportions of the bee community with ecologically relevant traits that continued to visit flowers in two different trait groups following floral manipulation. This was true despite different predictability of the bee morphospecies identities that visited the two floral trait groups. If replicable over larger spatial and temporal scales, this strategy may allow estimates of ecological function. In agriculture, trait ‘matching’ of tongue-length and corolla depth is more linked to fruit set than species or trait diversity [21]. Thus, relative trait group composition may be more relevant for understanding ecosystem function. This experiment thus sets the stage for longer-term, landscape-scale studies.

In this study, each flower trait group was still available elsewhere in the field. Bees were slightly less faithful in manipulations, but maintained trait group partners overall. If floral trait compositions changed in entire fields or landscapes, bees might more drastically adapt their foraging patterns (e.g. [1]). Contrary to my hypothesis, long-tongued bees were more faithful foragers instead of forming novel interactions. Many long-tongued bees were also larger-bodied [13], so may be more competitive [8], or energetically requiring higher nectar volumes or qualities only provided here by tube flowers, explaining their underrepresentation on open flowers [14]. The higher diversity of the mostly short-tongued bees on open flowers may explain their lower predictability (figure 2c). Continuing research on which traits allow reliable predictions and at which spatial and temporal scales they are predictive is a major challenge for trait-based network ecology.

**Table 2.** Generalized linear mixed models. Run with a binomial error and logit link; estimate is the proportion of bees in a manipulated patch with long tongues.

| model 1        | estimate | s.e. | z-value | Pr(>|z|) |
|----------------|----------|------|---------|----------|
| controls       | 0.653    | 0.398| 1.64    | 0.101    |
| tube removal   | 0.86     | 0.05 | 17.44   | less than 0.001 |
| open removal   | −1.299   | 0.05 | −25.23  | less than 0.001 |
| model 2        |          |      |         |          |
| (intercept)    | 2.486    | 0.487| 5.11    | less than 0.001 |
| tube removal   | −3.38    | 0.999| −34.26  | less than 0.001 |
| observed       | −0.88    | 0.074| −11.92  | less than 0.001 |
| tube removal × observed | 1.05 | 0.113| 9.30    | less than 0.001 |

<table>
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**Ethics.** Methods adhered to Yale University standards and required no permits.

**Data accessibility.** All raw data are available in electronic supplementary material, table S2.

**Competing interests.** I declare I have no competing interests.

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References