

mortality or breeding phenology, including frequency of winter reproduction, should be part of future research, as should quantifying vegetation quality that could reflect, for example, continent-scale long-term variation in climate or nutrient deposition.

Irrespective of the proximate process (or processes) affecting winter population growth rate, the coherence of the changes coinciding with a period of ongoing global environmental change suggests increasingly frequent prolonged periods of low amplitude, although high-amplitude vole peaks—as seen in 2011 in northern Fennoscandia—may occasionally reappear. The loss of years of super-abundant voles could reduce zoonotic disease risk and crop damage (27). Continent-scale collapses in population cycles are likely to be deleterious for vole predators because for most, reproduction is modulated by vole density in spring, which is when the strongest and most consistent dampening occurs. Large impacts on vegetation (6) and predator populations (1, 28) could see cascading effects on other compartments of the food webs (3, 29) in ecosystems as diverse as farmland, forest, and arctic tundra.

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Supplementary Materials

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Detection and Learning of Floral Electric Fields by Bumblebees

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Insects use several senses to forage, detecting floral cues such as color, shape, pattern, and volatiles. We report a formerly unappreciated sensory modality in bumblebees (*Bombus terrestris*), detection of floral electric fields. These fields act as floral cues, which are affected by the visit of naturally charged bees. Like visual cues, floral electric fields exhibit variations in pattern and structure, which can be discriminated by bumblebees. We also show that such electric field information contributes to the complex array of floral cues that together improve a pollinator's memory of floral rewards. Because floral electric fields can change within seconds, this sensory modality may facilitate rapid and dynamic communication between flowers and their pollinators.

Flowers produce a diverse range of cues and attractants to pollinators and in doing so act as sensory billboards (1). The diversity of floral cues encompasses intricate color hues and patterns, petal texture, fragrant volatiles, local air humidity, and echolocation fingerprints (1–4). The impact of floral cues on pollinator behavior has been observed since Aristotle (5), yet new floral cues are still being discovered (3, 4). Multimodal floral cues have been found to enhance both pollinator foraging efficiency and

pollination (6), and thus facilitate increased seed and fruit set.

Flying insects, including pollinators like honeybees, usually possess a positive electric potential (7–10). Conversely, flowers often exhibit a negative potential (7, 11). Electric fields arising as a result of this potential difference between flowers and insects promote pollen transfer and adhesion over short distances (7, 8, 12, 13). Furthermore, these fields differ according to the pollination status of the flower, as the deposition of pollen and resulting pollination changes flower electric potential (14, 15). However, the use of electric fields by pollinators as informative cues has not been investigated. In the complex world of plant-pollinator interactions, any

cue that increases pollination and foraging efficiency should be mutually beneficial. Here, we report that bumblebees can detect and learn to use floral electric fields, and their structural variation, to assess floral reward and discriminate among flowers.

The electrical interactions between the bee and the flower arise from the charge carried by the bee and the potential of the flower in relation to the atmospheric electric field. To quantify bee charge, individual *B. terrestris* workers were trained to fly into a Faraday pail that contained a sucrose reward. The net charge q carried by the bee was measured from the induced voltage on a calibrated capacitor (methodology described in supplementary materials). Measured on 51 individuals, 94% of bees were positively charged and 6% negatively charged ($q_{\text{mean}} = 32 \pm 5$ pC, SD = 35pC) (Fig. 1A). These results corroborate previous measurements on the honeybee *Apis mellifera* (9) and establish that the majority of bees flying in the arena carry a positive charge susceptible to transfer.

Electrical interaction between bee and flower was further explored by placing *Petunia integrifolia* flowers in an arena with free-flying foraging bees. The electric potential in *Petunia* stems was recorded to assess the electrical signature produced by the approach and landing of an individual charged bee. Charge transfer to the flower resulted in a positive change in electric potential recorded in the stem. The landing of 50 indi-

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viduals resulted in a mean potential change lasting ~100 s, which peaked at -25 ± 3 mV (SD = 24, $n = 50$) (Fig. 1B). Such change exceeds natural fluctuations in the absence of bees (Fig. 1B) and outlasts the presence of the bee on the flower. This change in potential is often initiated before contact with the bee (movie S1), suggesting that this is not simply a hydraulic wound-response variation potential as in (16) but involves direct electrostatic induction between the charged bee and the grounded flower as hypothesized in (7, 8).

Because the floral electric potential is directly affected by pollination (14, 15) and bee visitation (Fig. 1B), it potentially carries information for other visiting pollinators regarding floral resources. Visiting pollinators affect floral cues directly, by leaving scent marks on the petal surface, or by initiating changes in floral cues, such as color, shape, and humidity (4, 17–19). Such changes typically occur in the time frame of minutes to hours. The variation potential produced by bee visitation occurs within a time frame of seconds (Fig. 1B).

For a floral electric field to act as a cue, it must be possible for pollinators to detect and

discriminate it from the background. We used differential conditioning (3) to test the ability of bumblebees to discriminate between artificial flowers (E-flowers) with differing electric fields. E-flowers consisted of a 35-mm-diameter by 1.5-mm-thick steel base disk decorated with a purple epoxy top disk. Half the E-flowers were held at a biologically relevant 30-V dc bias voltage. This voltage was chosen as a proxy for the electric field of an isolated flower standing 30-cm tall in a typical 100 V m^{-1} atmospheric electric field (20). Charged E-flowers offered a sucrose reward, while identical E-flowers were held at ground (0 V) and provided a bitter quinine hemisulfate solution (3). E-flowers were indistinguishable in every other respect. During the course of 50 bee visits, there was an increase in the relative number of visits to rewarding charged flowers (Fig. 2A). To measure bee learning, we compared the mean accuracy of the final 10 visits (visit 41 to 50) to a random choice model. In their final 10 visits to 30-V charged E-flowers, bees ($n = 11$) achieved $81 \pm 3\%$ accuracy ($T_{1\text{-sample}} = 10.8, P = 7.4 \times 10^{-7}$). Both flower types were then grounded and the choice test continued. Without the electric cue, the same

set of trained bees could no longer discriminate between the rewarding and unrewarding E-flowers, also demonstrating the absence of systematic experimental bias. Accuracy after the electric cue is removed was $54 \pm 4\%$, which does not differ significantly from random choice ($T_{1\text{-sample}}=1, P = 0.35$) (Fig. 1B). Using a 10-V bias failed to elicit significant learning ($n = 10$, mean accuracy = $56 \pm 4\%$, $T_{1\text{-sample}} = 1.4, P = 0.19$) (Fig. 2, A and B).

Floral cues are diverse and address the multimodal perception of pollinators. Working in concert, floral cues enhance foraging efficiency (6) and constitute a complex informational ecology of competing flower advertisement. Color cues rely both on hue and on contrast between hues and their geometrical patterns. Nectar guides constitute such patterns, providing information attractive to pollinators and facilitating foraging efforts (21, 22). By analogy, the geometry of floral electric fields may carry additional information important for pollinators. The diversity of floral electric field geometry can be experimentally visualized by coating flowers with positively charged colored particles released as an aerosol close to the corolla. The heterogeneous

Fig. 1. Electric charge carried by bumblebees and its transfer to flowers.

(A) Histogram of electric charge of flying bumblebees. Boxplot shows median, SD, interquartile range, and outliers. (B) Mean variation potential in the *Petunia* stem resulting from bee landings (red, $n = 51$), shown with ± 1 SEM (gray). Distribution of the natural variation of stem potential (measured along 35 samples of 30 s) in absence of bees, truncated at 2 SD (blue).

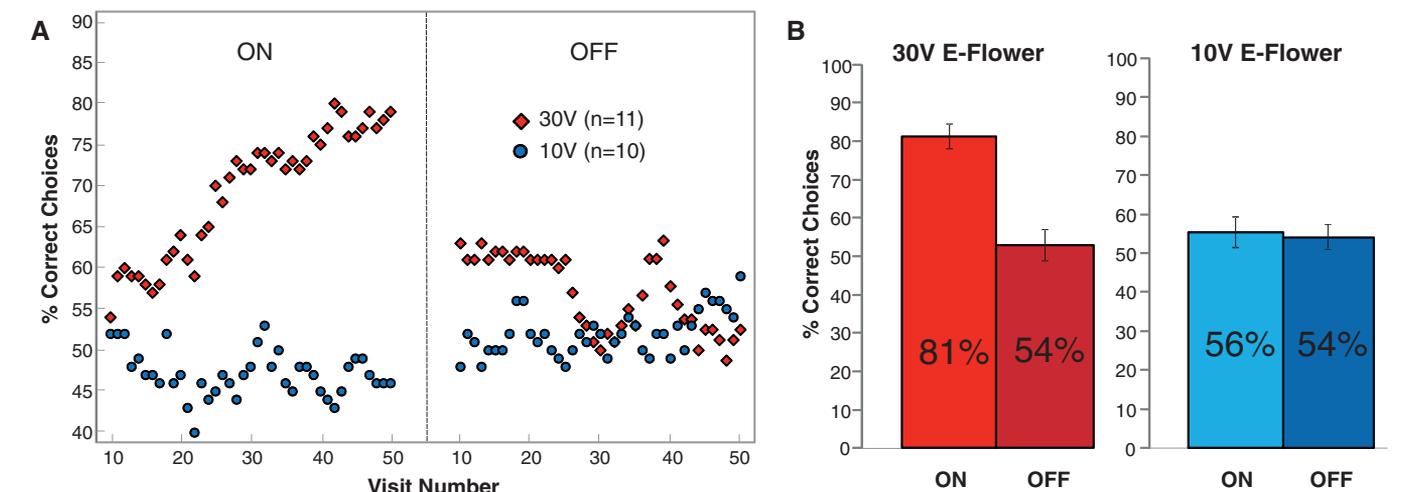
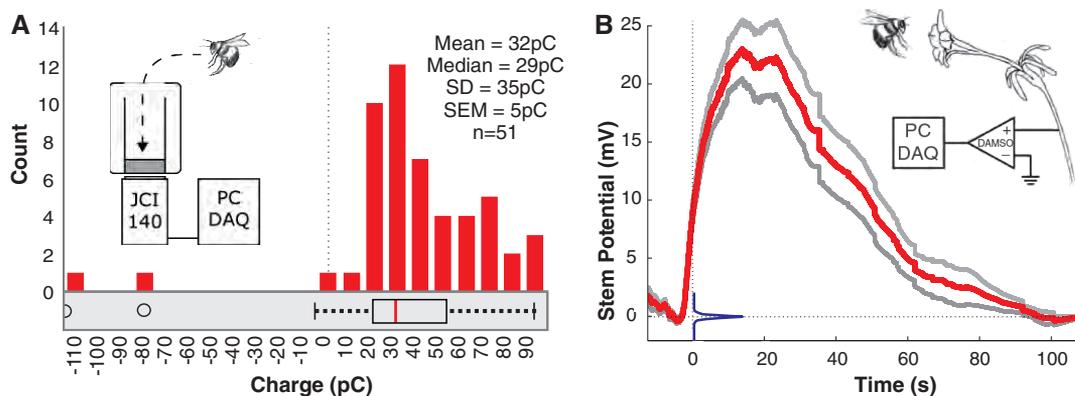


Fig. 2. Bumblebees learn the presence of an electric field. (A) Learning curves of foraging bees, trained to 30-V (red diamonds) or 10-V (blue circles) E-flowers. Dashed line shows switching off electric field. (B) Mean correct choices to 30-V (left) and 10-V (right) E-flowers over visits 41 to 50 in (A) during training (voltage on) and control (voltage off). Error bars show SEM.

Fig. 3. Geometry of floral electric field and discrimination task. (A) Flowers before (left half) and after (right) spraying with electrostatic colored powder; (a) *Gerbera hybrida*, (b) *Digitalis purpurea*, (c) *Geranium magnificum*, (d) *Calibrachoa hybrida*, (e) *Petunia hybrida*, (f) *Clematis armandii*. Density of powder deposition reflects the variation in electric field strength at the flowers' surface. (B) FE model of an idealized 30-cm-tall flower, equipotential with ground, in an atmospheric field of 100 V/m. Left: scalar electric potential. Right: electric field magnitude. (C) FE models of electric field produced by E-flowers. (D) Color scale for (B) and (C). (E) Pattern discrimination as mean percentage of correct choices over the last 10 visits for patterns on and off. Error bars show SEM.

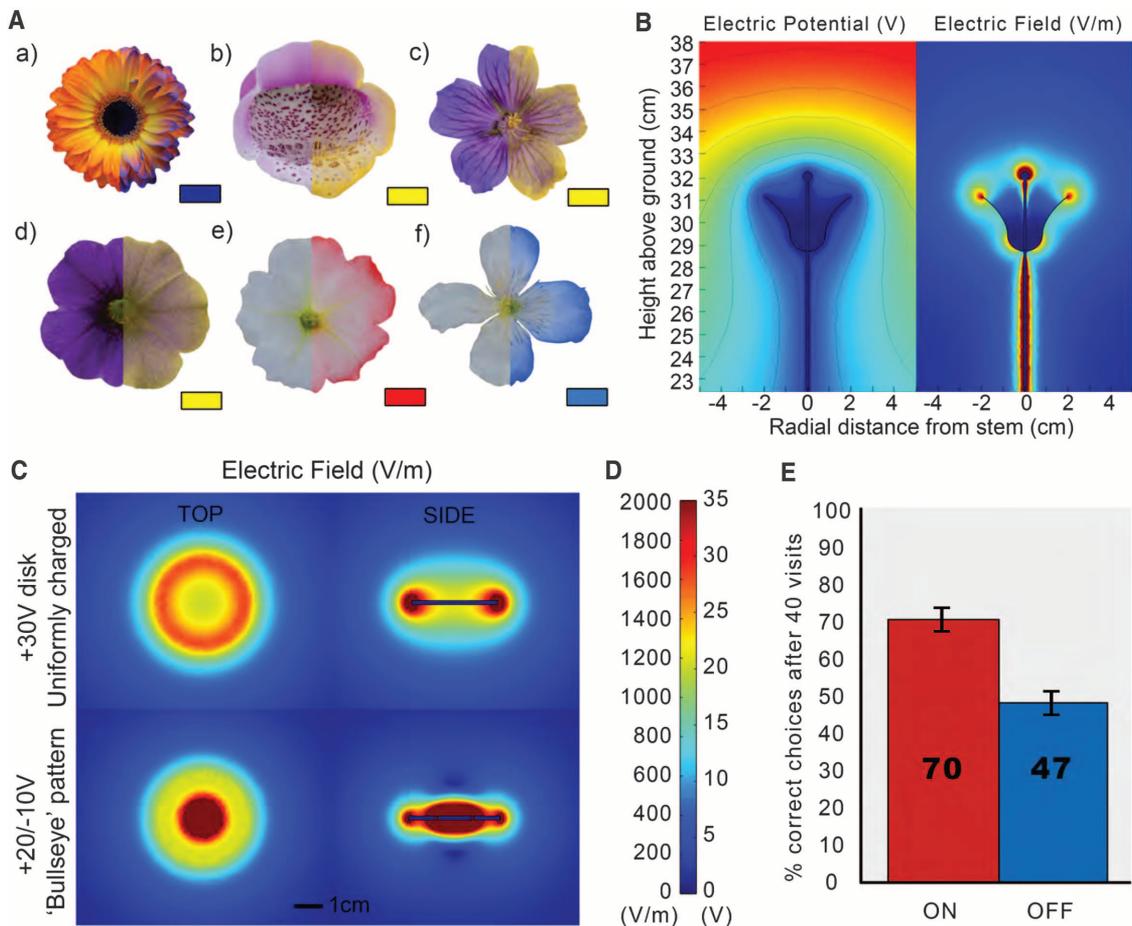
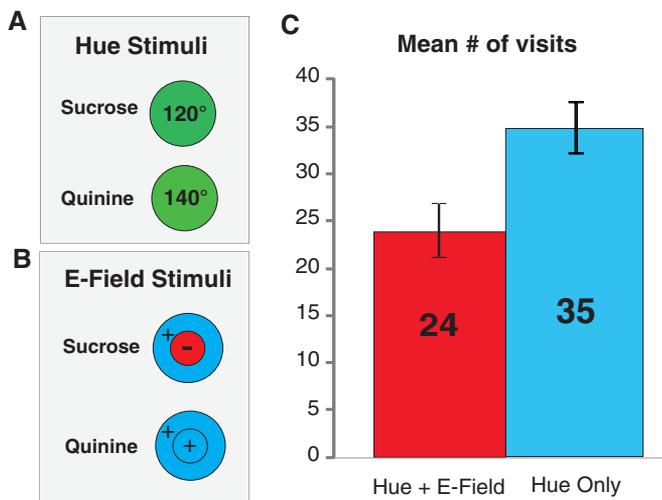


Fig. 4. Multimodal facilitation. Colors (A) and voltage configurations (B) associated with rewarding and aversive E-flowers. (C) Mean number of visits taken by bees in each group to reach 80% correct choices.



pattern of color deposition reveals the structure of the electric field at the flower's surface (Fig. 3A).

Electric field structure was also visualized using finite element (FE) modeling of an idealized 30-cm-tall flower in a physically realistic, 100 V m⁻¹ atmospheric electric field (20) (Fig. 3B, left). Plants are conductively linked to ground via their stems and roots, a connection that maintains them close to ground poten-

tial (7). Hence, a grounded 30-cm-tall plant in such an atmospheric electric field exhibits a 30-V potential difference between its inflorescent structures and the surrounding air, exhibiting a patterned electric field (Fig. 3B). This experimental and modeling evidence reveals that flower morphology determines electric field geometry.

To test the bee's ability to discriminate E-field geometries, differential conditioning was used

with two types of E-flowers, providing similar voltage but different local patterns (Fig. 3C). Rewarding E-flowers presented a bull's eye pattern, with the outer ring held at +20 V and the center ring at -10 V. Aversive E-flowers presented a homogeneous voltage at +20 V (Fig. 3C). Bees ($n = 10$) learned to discriminate between these two patterns, reaching $70 \pm 3\%$ accuracy over their final 10 visits, performing significantly better than random choice ($T_{1\text{-sample}} = 6.7, P = 8 \times 10^{-5}$) (Fig. 3E). After this task, a subset of the bees ($n = 4$) was allowed to complete 50 additional visits to rewarding and aversive E-flowers with identical homogeneous +20 V fields. These bees failed to discriminate between E-flowers (Fig. 3E). Altogether, these tests show that bumblebees can discriminate charged from uncharged flowers and can distinguish between flowers that differ in the geometry of their electric field. As such, E-fields could be used by flowers to provide information to their pollinators.

Floral cues can work individually or complementarily (1, 6). When presented together, multimodal cues enhance the certainty of sensory information used by honeybees. Specifically, the association of color with olfactory floral cues reduces the bees' perceptual uncertainty related to an individual floral cue and increases their ability to distinguish between rewarded

and aversive stimuli (23). The hypothesis can be formulated that the floral electric field reinforces the effectiveness of other floral cues. If true, an electric cue paired with a color cue should produce an enhanced learning outcome equivalent to that obtained with the test using color and scent. Differential conditioning was used to test this hypothesis. The same two green target hues were used as in (23), but olfactory cues were replaced with a patterned electric field (Fig. 3C). Bees were trained to discriminate between E-flowers of hue 120° HSB (hue, saturation, brightness) which offered a sucrose reward, and E-flowers of hue 140° HSB, which provided an aversive quinine solution (Fig. 4A). Bees learned to discriminate between the rewarding and aversive chargeless E-flowers either using color information alone ($n = 16$) or in combination with the patterned E-field ($n = 18$) (Fig. 4A). When learning color on its own, discrimination to 80% success (i.e., 8 out of the last 10 choices correct) took 35 ± 3 visits. When combined with the E-field pattern, the number of visits required was significantly reduced to 24 ± 3 ($T_{2\text{-sample}}; \text{unequal} = 2.86, P = 0.008$) (Fig. 4A). This demonstrates that the combination of two cues, E-field and hue, enhances the bee's ability to discriminate.

Our results show that electric field constitutes a floral cue. Contributing to a varied floral display aimed at pollinator senses, electric fields act to improve both speed and accuracy with which bees learn and discriminate rewarding resources. As such, electric field sensing constitutes a potentially important sensory modality, which should be considered alongside vision

and olfaction. The ubiquity of electric fields in nature and their integration into the bees' sensory ecology suggest that E-fields play a thus far unappreciated role in plant-insect interactions. The present study raises the possibility of reciprocal information transfer between plants and pollinators at time scales of milliseconds to seconds, much faster than previously described alterations in floral scent, color, or humidity (4, 18, 19). The remarkably accurate discrimination and learning of color patterns by bees was revealed by both laboratory and field training experiments (19, 21–23). Similarly, the present laboratory study reveals that floral electric fields occur in patterns and that they can be perceived. Hence, our study provides a framework for exploring the function and adaptive value of the perception of weak electric fields by bees in nature.

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Materials and Methods

References (24–26)

Movie S1

Data File S1

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Recovery of an Isolated Coral Reef System Following Severe Disturbance

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Coral reef recovery from major disturbance is hypothesized to depend on the arrival of propagules from nearby undisturbed reefs. Therefore, reefs isolated by distance or current patterns are thought to be highly vulnerable to catastrophic disturbance. We found that on an isolated reef system in north Western Australia, coral cover increased from 9% to 44% within 12 years of a coral bleaching event, despite a 94% reduction in larval supply for 6 years after the bleaching. The initial increase in coral cover was the result of high rates of growth and survival of remnant colonies, followed by a rapid increase in juvenile recruitment as colonies matured. We show that isolated reefs can recover from major disturbance, and that the benefits of their isolation from chronic anthropogenic pressures can outweigh the costs of limited connectivity.

Coral reefs are dynamic ecosystems periodically subjected to severe disturbances, such as cyclones, from which they typically recover at scales of one to two decades (1, 2). Today, this recovery is undermined by increasing anthropogenic pressures leading to global declines in coral cover (3, 4) and diversity (5, 6). Understanding the global degradation of coral reef ecosystems requires long-term data

on population and community dynamics, especially demographic processes (7–9). However, the rarity of such data has precluded a thorough assessment of the future of coral reef ecosystems in the IPCC report on climate change (10, 11), and current knowledge is mostly derived from studies of reef degradation (9, 12) rather than reef recovery. Here, we document the recovery of coral assemblages at Australia's largest oceanic reef

system, where changes in assemblage structure and key demographic parameters were quantified for 16 years, through a regime of disturbances beginning with a catastrophic mass bleaching event in 1998.

The Scott system of reefs is surrounded by oceanic waters on the edge of Western Australia's continental shelf. It is more than 250 km from the mainland and other reefs in the region, and more than 1000 km from a major center of urbanization (fig. S1). There is little fishing pressure at the reefs, apart from the harvesting of sea cucumber, trochus, and shark fin by Indonesian islanders using traditional fishing methods for more than 300 years (13, 14). Such oceanic reef systems may provide a critical refuge for coral reef assemblages because they are far removed from most direct anthropogenic pressures. Conversely, isolation and a consequent lack of connectivity may make such systems

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