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Glyphosate impairs collective thermoregulation in bumblebees

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Insects are facing a multitude of anthropogenic stressors, and the recent decline in their biodiversity is threatening ecosystems and economies across the globe. We investigated the impact of glyphosate, the most commonly used herbicide worldwide, on bumblebees. Bumblebee colonies maintain their brood at high temperatures via active thermogenesis, a prerequisite for colony growth and reproduction. Using a within-colony comparative approach to examine the effects of long-term glyphosate exposure on both individual and collective thermoregulation, we found that whereas effects are weak at the level of the individual, the collective ability to maintain the necessary high brood temperatures is decreased by more than 25% during periods of resource limitation. For pollinators in our heavily stressed ecosystems, glyphosate exposure carries hidden costs that have so far been largely overlooked.

The worldwide decline in insect biodiversity and abundance is well documented (*1*–*5*). Pollinating insects have not been spared from these impacts (*6*, *7*). Multiple, potentially interacting anthropogenic stressors are believed to be responsible, including habitat loss and fragmentation (*8*, *9*), pathogens, introduced species, climate change (*10*–*12*), and the increasing use of agrochemicals such as insecticides, fungicides, herbicides, and fertilizers (*9*, *13*).

Glyphosate, an organophosphorus herbicide that is highly effective and available at low production cost, has become the most widely applied herbicide since its commercial introduction in 1974 (*14*, *15*). Glyphosate kills plants by inhibiting one part of the shikimate pathway, 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS), an essential enzyme found in plants, fungi, and some bacteria (*16*). Because other organisms lack this enzyme, glyphosate was categorized as a "least toxic" (category IV) substance by the US Environmental Protection Agency (*17*) and consequently was long believed to be harmless for most animals, explicitly terrestrial insects such as bees (*18*). Standard risk assessment procedures for the approval of pesticides assess acute toxicity and are performed with well-fed, parasite-free individuals, removing naturally occurring stressors that may modulate the ability of bees to cope with pesticides (*9*). Under such "ideal" conditions, however, harmful nonlethal effects on individual physiology or behavior may easily be overlooked. In recent years, an increasing number of studies are reporting nonlethal, adverse effects of glyphosate on honey bee brood, on the sensory and cognitive abilities of adult honey bees (*19*–*23*), and on the bee gut microbiome (*24*–*26*). Whereas our knowledge of the effects of glyphosate on honey bees is still rudimentary at best, next to nothing is known about how glyphosate affects the roughly 20,000 species (*27*) of wild bees (*23*, *28*, *29*). Here, we investigated the effects of long-term glyphosate exposure on bumblebees (*Bombus terrestris*), especially when a second stressor, resource limitation, co-occurs.

Bumblebees increasingly serve as surrogate species representing wild bees in ecotoxicological studies (*30*). They live in annual colonies of up to several hundred individuals and are excellent pollinators for a vast array of plant species. Partly because of their unusual ability to show facultative endothermy (i.e., the ability to actively elevate their thorax temperature), bumblebees are abundant in temperate regions, visiting flowers even under harsh weather conditions (*31*). Thermogenesis consumes nearly as much energy as flight (*31*–*33*) and is important for flight muscle activation (*34*) as well as brood incubation (Fig. 1A). In a highly integrated process, bumblebee colonies maintain their brood at elevated and stable temperatures of ~30° to 35°C (*31*, *35*, *36*), enabling rapid brood development and colony growth (*31*).

Bumblebee colonies are known to show large intercolony variability (*37*), complicating studies on colony-level effects. We analyzed all glyphosate treatment effects in within-colony comparisons, thus removing the obscuring effect of intercolony variability. Fifteen bumblebee colonies were maintained in the laboratory. Each colony was divided into two halves separated by a wire mesh (Fig. 2A and fig. S2A). Queens were switched between colony sides daily (providing queen presence and brood of all stages on both sides of a colony), and the two sides of a colony were regularly balanced in number of workers (supplementary materials and fig. S3). In a blinded experimental approach, colonies were fed daily, receiving pure sugar water on one side (50% w/w; "Control"; N = 15) and the same amount of the sugar water containing glyphosate (5 mg/liter) on the other side ("GLY"; N = 15). This glyphosate concentration is in the middle range of concentrations used in previous feeding studies on honey bees—ranging between 0.25 mg/liter and 10 mg/liter [e.g., (*38*–*40*); reviewed in (*19*); see supplementary materials]—and is the lower of two concentrations shown to negatively affect gut microbiota in honey bees (*24*). We analyzed all treatment effects using a Bayesian approach. We report means with 95% credible intervals (CrI), and differences between glyphosate-treated and Control colony sides with 95% CrIs and certainties of difference (CDs). We regard CDs between 90% and 95% as providing weak statistical support, and CDs of 95% or higher as strong statistical support. Workers from glyphosate-treated colony sides showed a reduced life expectancy (by 1.9 days; 95% CrI, −0.1 to 3.9 days) relative to the Control side (CD > 97%; fig. S4). However, mean life expectancy for workers from both treatment groups was at least 32 days; hence, glyphosate can be considered sublethal at the concentration used in this study, mirroring findings for honey bees (*19*).

To investigate whether glyphosate affects individual investment into brood incubation, we tested 305 workers from Control and glyphosate-treated colony sides in test arenas with brood dummies (temperature-controlled aluminum cones mimicking pupae; Fig. 1, A and B, supplementary materials, and fig. S2B) (*41*–*43*). Bees were tested individually, either with or without sugar water available in test arenas. Bees from glyphosate-treated colony sides tended to invest less time in incubation relative to their non–glyphosate-exposed nestmates (on average 12% less time; CD = 90%; 95% CrI, −35 to 161 s; Fig. 1C and fig. S5), even when ample sugar water was provided in test arenas. Glyphosate exposure did not affect incubation probability in this experimental setting (CD with sugar water, <66%; without sugar water, <84%). However, incubation probability was strongly modulated by sugar water availability itself: When bees did not find sugar water in the test arena, their probability of showing incubation behavior decreased [Control, by 50%; GLY, by 67%; CD > 99% for both Control (−0.31; 95% CrI, −0.55 to −0.03) and glyphosate-treated workers (−0.41; 95% CrI, −0.61 to −0.14); Fig. 1D]. These results suggest that information on sugar water availability is integrated into individual response decisions. Our findings provide weak statistical support for a decrease in individual investment into the task of brood incubation in glyphosate-exposed workers, even at large sample sizes.

The highly consequential impact of long-term glyphosate exposure becomes evident

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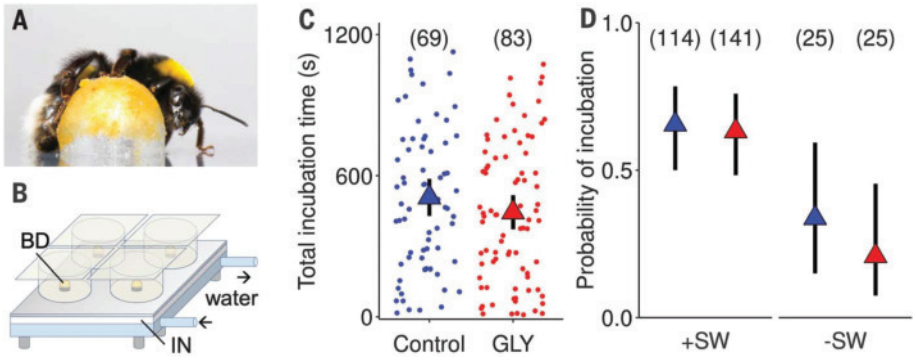

Fig. 1. Effects of long-term glyphosate exposure on individual brood incubation. (**A**) Bumblebee on brood dummy covered with brood wax. (**B**) Temperature-controlled brood dummies (BD) attached to heating plate and water bath; test arena floor isolated by insulation layer (IN). (**C**) Time spent incubating is 12% lower in glyphosate-exposed workers (red) than in nonexposed workers (blue) (64 s less; 95% CrI, −35 to 161 s; CD = 90%). Results based on linear mixed model (LMM) with treatment as fixed effect and taking colony origin into account. Dots: total individual incubation time; triangles: estimated mean total incubation time; whiskers: 95% CrI. Workers tested with sugar water available in test arena. (When tested without sugar water, low incubation probability resulted in small sample size; data shown in fig. S5.) (**D**) Incubation probability is lower in workers tested without sugar water (−SW) available in test arenas compared to workers tested with sugar water (+SW) available (certainty of difference: >99%) for both nonexposed (blue; −0.31; 95% CrI, −0.55 to −0.03) and glyphosate-exposed workers (red; −0.41; 95% CrI, −0.61 to −0.14). Results are based on binomial generalized LMM with treatment and sugar water availability as fixed effects, including the (nonsignificant) interaction term and taking colony origin into account. Glyphosate has no strong effect on incubation probability (CD, +SW < 66%, −SW < 84%). Triangles: estimated mean incubation probability; whiskers: 95% CrI; sample sizes in brackets.

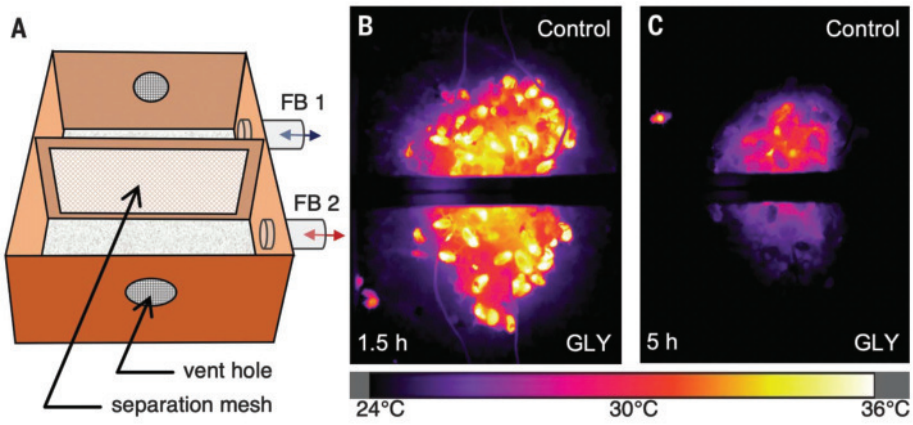

Fig. 2. (**A**) **Split-colony box.** Colonies were divided in half by a separation mesh; the two colony sides contained the same amount of brood and workers. Sugar water was provided in attached feeding boxes (FB1 and FB2, not shown) that could be accessed via plexiglass tubes. In the feeding boxes, one colony side received sugar water (Control, blue arrow); the other side received sugar water containing glyphosate (GLY, red arrow). (**B** and **C**) False-color thermal image of a split colony 90 min (B) and 5 hours (C) into a resource limitation stress test. Nonexposed (Control) and glyphosate-exposed (GLY) sides of colony D are shown; it has 65 workers per colony side.

when investigating thermal ability at the colony level. Nest temperatures were recorded using a thermal camera (which reliably reflects brood temperatures; Fig. 2B and fig. S6). First, we analyzed mean nest temperatures. When colonies were undisturbed and well-fed, no difference in mean nest temperature between the two sides of a colony was detected (CD = 55%; figs. S7 and S8). However, when colonies experienced resource limitation (see supplementary materials), effects of glyphosate exposure became evident. Glyphosate-treated colony sides showed a strong impairment in collective thermoregulation (Fig. 3). Mean nest temperatures declined more rapidly in glyphosate-treated colony sides than in Control sides (Fig. 3A and figs. S9 and S10A): In the majority of tested colonies, the glyphosate-treated side dropped to mean nest temperature below 28°C before the Control side of the colony did (10 of 13 colonies; fig. S9). On average, glyphosate-treated colony sides were able to maintain their mean nest temperature above 28°C for 26% less time than their nonexposed colony side (−1 hour; CD > 99%; 95% CrI, 0.2 to 2.2 hours; Fig. 3B and fig. S9).

Next, we analyzed the change in nest area that is maintained above 28°C; this allowed us to control for potential differences between colony sides (i.e., in amount of brood). Again, when facing resource limitation, the decline in area at optimal brood temperature was faster in the glyphosate-treated colony sides (Fig. 3C and fig. S10B): In the majority of tested colonies, the glyphosate-treated colony sides had no nest region at temperatures above 28°C, whereas the Control sides were still able to maintain parts of their nest above 28°C (8 of 13 colonies). On average, the time during which glyphosate-treated colony sides were able to maintain at least 40% of the original area above 28°C was 21% shorter than in the Control colony sides (−0.9 hours; CD > 96%; 95% CrI, −0.1 to 2.4 hours; Fig. 3D). Our results document a robust pattern even for a limited sample size: When colonies experience resource limitation, glyphosate strongly impairs their ability to maintain their brood at high brood temperatures.

Temperature is the most important factor in insect development (*44*, *45*); suboptimal brood temperatures have been shown to affect sensory and cognitive abilities of adults [honeybees (*46*–*48*)]. To directly assess the effect of temperature on survival and development of bumblebee brood, we raised 186 bumblebee pupae in incubators at different constant temperatures (see supplementary materials). Survival rate is high and developmental time is short only within the narrow range of 28° to 35°C (Fig. 4). Already at 25°C, survival is reduced to 17% and developmental rate decreases by more than 50% relative to maximum rates. Clearly, thermogenesis and brood incubation are essential for bumblebee brood production and colony growth. Any impairment of this process will directly affect colony fitness. Rapid brood development and colony growth are a prerequisite for reproduction; colonies will invest into the production of queens only if a certain colony size is reached (*31*, *49*, *50*). The larger the colony is at this point, the higher its chances of successfully producing queens (*50*). For bumblebees, the primary cost of suboptimal brood temperatures is a time loss. In a short growing season, developmental delays and loss of brood often cannot be compensated for, and this will consequently reduce colony growth and colony fitness (*50*). The precise impact of an impairment in collective thermoregulation will vary depending both on ambient temperature and on the degree of resource limitation experienced. On the basis of our

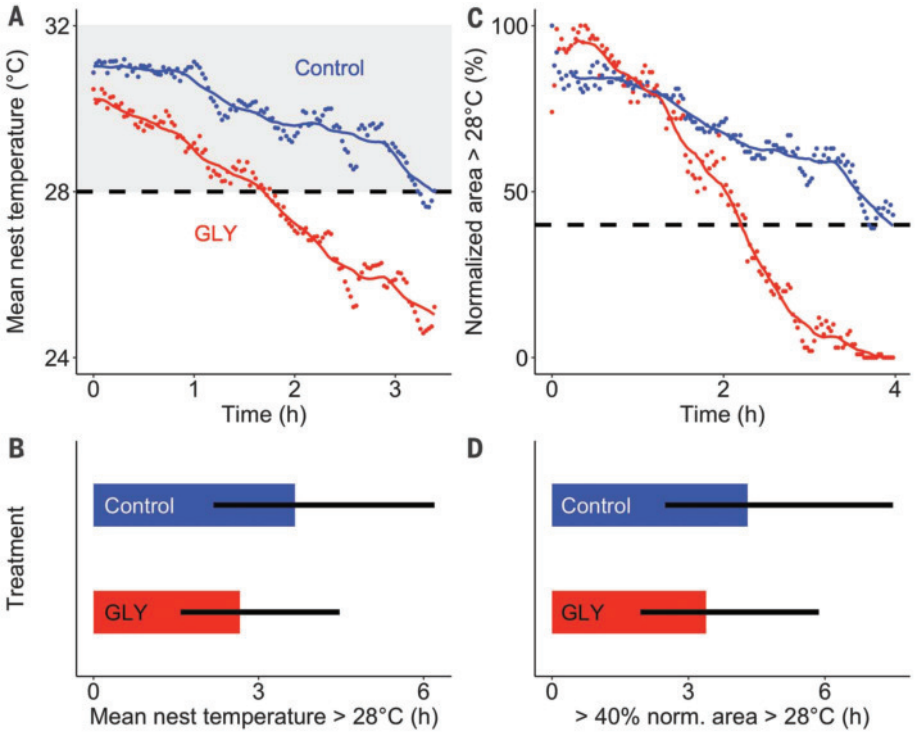

Fig. 3. Long-term glyphosate exposure reduces collective thermoregulation ability when resources are limited. (**A**) Example of mean nest temperature (MNT) during resource limitation stress test in nonexposed (Control, blue) and glyphosate-exposed (GLY, red) sides of colony F. Dots: MNT; lines: MNT averaged over a running window of ~30 min; shaded area: optimal brood temperature; dashed line: 28°C threshold used for analysis shown in (B). (**B**) Glyphosate-treated colony sides maintained MNT above 28°C less long (26% shorter) relative to Control colony sides during resource limitation stress tests (CD > 99%; 1 hour less; 95% CrI, 0.2 to 2.2 hours). Results based on LMM with log-transformed time as response, treatment as fixed effect and accounting for colony identity. Bars: estimates; whiskers: 95% CrI. (**C**) Example of normalized nest area (NNA) maintained >28°C during resource limitation stress test, based on same data shown in (A). To exclude differences in amount and distribution of brood, maximum area >28°C during the first hour of a stress test was determined for each colony side; time to reduction to 40% of this area (dashed line) was analyzed [see (D)]. Dots: percentage of NNA maintained >28°C; lines: NNA averaged over a running window of ~30 min. (**D**) Glyphosate-treated colony sides maintained warm NNA (at least 40% of NNA >28°C) less long (21% shorter) compared to Control colony sides during resource limitation stress tests (certainty of difference, >96%; 0.9 hours less; 95% CrI, −0.1 to 2.4 hours). Results based on LMM with log-transformed time as response, treatment as fixed effect and accounting for colony identity. Bars, estimates; whiskers, 95% CrI; *N* = 13.

data (Fig. 4B), we developed a model that allows for further exploration of the effects of a reduced incubation ability (by 26% as documented in our study) on colony growth in different environmental scenarios (figs. S1.1 to S1.4). Our findings show a strong impact, especially when ambient temperatures are low (fig. S1.4). This suggests that the effects of glyphosate on colony fitness may be especially potent under cold stress (e.g., in early spring), when solitary queens raise their first brood alone, and in the early phase of colony development, when colonies are still small.

It is important to emphasize that under standard laboratory conditions, the detrimental effects of glyphosate exposure on collective thermoregulation as documented in this study would remain hidden. When tested for the impact of agrochemicals, colonies and individuals are usually well-fed, enabling them to compensate for subtle shifts in energy requirement (*51*). Colonies in our study also received ample amounts of sugar water daily (text S1), except during resource limitation tests, and we found no difference in measured parameters of colony development or in worker size (figs. S11 to S13). However, we did find support for glyphosate-induced compensatory sugar water uptake. Glyphosate-treated colony sides consumed more of the provided sugar water per day (fig. S14); 24 hours after feeding, they were more likely to have fewer filled honey pots left relative to Control sides (CD > 99%; glyphosate 95% CrI, 0.72 to 0.89; Control 95% CrI, 0.64 to 0.85). Compensatory resource intake has also been shown following immune system activation in bumblebee workers (*52*, *53*). Bumblebee colonies frequently face a trade-off between foraging and brood incubation (*31*, *54*). Individual task selection is modulated by resource availability (Fig. 1D). When no sugar water is available, individual incubation probability decreases, potentially freeing up workers for the task of foraging. Workers in the glyphosate-treated colony sides may have reached this point sooner, and thus stopped incubating earlier, as a result of increased compensatory sugar water consumption and/or reduced efficiency of nutritional intake. However, we never observed a shift to foraging, as neither glyphosate-treated nor Control bees moved off the nest or into the foraging boxes during resource limitation tests.

Under natural conditions, stressors rarely act in isolation. Bumblebees are often chronically exposed to cocktails of agrochemicals both during development and as adults (*9*), and they are regularly confronted with periods of low or no nectar availability due to bad weather conditions or low forage availability (*55*). When honey stores are depleted, colony temperature drops, susceptibility to parasites and pathogens increases (*50*), and foraging activity and ultimately colony growth and reproductive performance is impeded (*55*–*59*). Resource limitation is especially and increasingly problematic in agricultural landscapes (*55*, *59*), where pollinators also encounter the largest pesticide load (*13*). Glyphosate exposure will exacerbate the challenges bumblebees face by presenting a hidden survival cost that is continuously paid to maintain colony growth.

Detrimental effects on thermogenesis have also been reported for neonicotinoids [honey bees (*60*–*62*), bumblebees (*63*); and solitary bees (*64*)]. Whereas the direct impacts of neurotoxic insecticides on bee health and behavior are easier to understand (*65*), the proximate mechanisms of glyphosate and how it affects bumblebee metabolism, behavior, and thermogenesis remain to be fully investigated. Gut dysbiosis as a consequence of glyphosate exposure has been shown in honey bees (*24*), and because the honey bee and bumblebee gut microbiomes are similar (*66*–*68*), this may play an important role in the impairments we observed. Gut bacteria are important for the breakdown of nutrition, for neutralization of dietary toxins, and as a defense against parasites (*69*, *70*). Although a perturbation of gut microbiota is unlikely to produce an immediate, obvious increase in bee lethality, more subtle effects such as nutritional deprivation, loss of efficiency in the process of thermogenesis, and the need for compensatory resource intake are likely to occur (*24*, *71*). Glyphosate may also disrupt some fundamental property of the social system. Individual behavior is embedded in and shaped by the social context (*72*), and numerous feedback

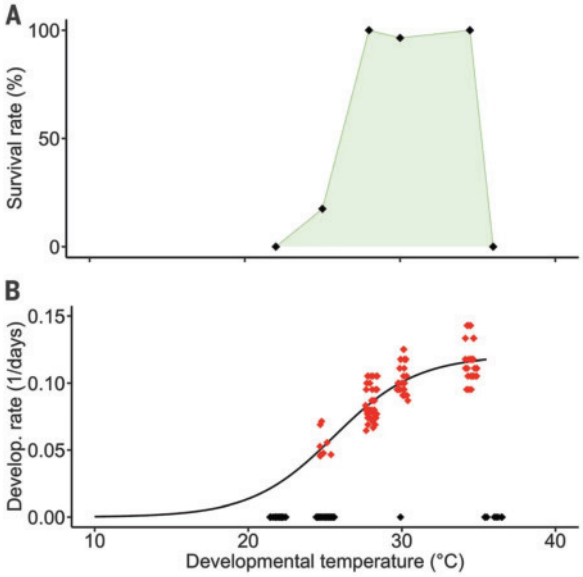

Fig. 4. Effect of temperature on survival and developmental time in bumblebee pupae. (**A**) Successful brood development depends on temperature: Pupae maintained at different constant temperatures develop into adults only in the range of 25° to 35°C. Survival is high (>95%) for temperatures between 28° and 34.5°C. None of the pupae at 22°C or at 36°C survived. Black diamonds: % pupae that developed into adult; N = 38 (22°C), 46 (25°C), 36 (28°C), 28 (30°C), 30 (34.5°C), and 8 (36°C). (**B**) Pupal developmental rate depends on temperature and is described by the model: Developmental rate = D_{max}/{1 + exp [−(temperature − T_{min})/k]}. For pupae that developed into adults [red diamonds, excluding pupae that died (black diamonds)], we obtained D_{max} = 0.12 (maximal developmental rate in days^{-1}), T_{min} = 25.6°C (lower temperature limit), and k = 2.70°C (width parameter of the lower temperature limit). Similar to survival (A), developmental rate is high only in a narrow temperature range.

processes integrate individual behavior into a collective, functional unit (*73*). In bumblebees, individual thermal response behavior is strongly modulated by the social environment (*42*). Although insect colonies are famous for their ability to buffer internal and external fluctuations (*74*), collective flexibility and resilience may differ between species (*75*) and reach limits when stressors accumulate and cause even minute impairments at the level of the individual, affecting their ability to sense and adequately respond to social and environmental information.

Our study highlights the importance of (i) identifying appropriate behavioral metrics and (ii) taking additional stressors and the natural context into account when establishing risk assessment procedures (*76*). Direct lethal effects draw the strongest public attention and are easily shown experimentally. Subtle, nonlethal alterations in individual behavior are harder to detect and will often remain hidden, especially under standard testing procedures when behavior is assessed outside of its natural (social) context. For social species, identifying critical collective readouts is crucial.

Glyphosate threatens bumblebees not only indirectly by reducing the availability of wild flowers but also directly by impairing a key collective behavior, the colony's ability to maintain its brood at beneficial temperatures during periods of limited resource availability. By 2020, the projected usage of glyphosate was estimated to be 1 million tons/year (*15*). It is now ubiquitous in food, water, air, and even human urine (*77*). Glyphosate is the active substance in numerous herbicide formulations, with coformulants (e.g., in products such as RoundUp) often posing additional risks (*20*, *78*, *79*). The absence of validated higher-tier testing methodologies for wild bees has so far presented a challenge in performing meaningful risk assessments for these non-target pollinators. Our study opens a promising avenue for developing new test protocols, which are urgently needed in order to make informed decisions about the costs and benefits of our future use of glyphosate-based and other agrochemicals.

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