Modeling scale up of anthropogenic impacts from individual pollinator behavior to pollination systems

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Abstract
Understanding how anthropogenic disturbances affect plant–pollinator systems has important implications for the conservation of biodiversity and ecosystem functioning. Previous laboratory studies show that pesticides and pathogens, which have been implicated in the rapid global decline of pollinators over recent years, can impair behavioral processes needed for pollinators to adaptively exploit floral resources and effectively transfer pollen among plants. However, the potential for these sublethal stressor effects on pollinator–plant interactions at the individual level to scale up into changes to the dynamics of wild plant and pollinator populations at the system level remains unclear. We developed an empirically parameterized agent-based model of a bumblebee pollination system called SimBee to test for effects of stressor-induced decreases in the memory capacity and information processing speed of individual foragers on bee abundance (scenario 1), plant diversity (scenario 2), and bee–plant system stability (scenario 3) over 20 virtual seasons. Modeling of a simple pollination network of a bumblebee and four co-flowering bee-pollinated plant species indicated that bee decline and plant species extinction events could occur when only 25% of the forager population showed cognitive impairment. Higher percentages of impairment caused 50% bee loss in just five virtual seasons and system-wide extinction events in less than 20 virtual seasons under some conditions. Plant species extinctions occurred regardless of bee population size, indicating that stressor-induced changes to pollinator behavior alone could drive species loss from plant communities. These findings indicate that sublethal stressor effects on pollinator behavioral mechanisms, although seemingly insignificant at the level of individuals, have the cumulative potential in principle to degrade plant–pollinator species interactions at the system level. Our work highlights the importance of an agent-based modeling approach for the identification and mitigation of anthropogenic impacts on plant–pollinator systems.

KEYWORDS
agent-based model, behavior, bumblebee, foraging, memory, plant–pollinator interactions, pollen transfer, simulation

Aumento en el Modelado de los Impactos Antropogénicos de Polinizador Individual a Sistemas de Polinización

Resumen: El entendimiento de cómo las perturbaciones antropogénicas afectan a los sistemas planta-polinizador tiene consecuencias importantes para la conservación de la biodiversidad y el funcionamiento del ecosistema. Los estudios previos realizados en laboratorios muestran que los pesticidas y los patógenos, los cuales han estado implicados en la rápida declinación global de los polinizadores en los años recientes, pueden perjudicar los procesos de comportamiento necesarios para que los polinizadores exploten...
adaptively the resources florals and transfer in a matter of effective the pollen between the plants. Sin embargo, todavía no está claro el potencial de que estos efectos estresantes subletra sobre las interacciones planta-polinizador a nivel individual secan a cambios en las dinámicas de las plantas y las poblaciones silvestres de polinizadores a nivel de sistema. Desarrollamos un modelo basado en el agente y con parámetros empíricos para un sistema de polinización de abejo de llamado SimBee. Con él analizamos los efectos de las disminuciones inducidas por estresantes sobre la capacidad de memoria y la velocidad de procesamiento de información de los forrajeros individuales en la abundancia de abejas (escenario 1), diversidad de plantas (escenario 2) y la estabilidad en el sistema abeja-planta (escenario 3) durante 20 temporadas virtuales. El modeloado de una red simple de polinización de un abejo y cuatro especies de plantas con floración a la par y polinizadas por abejas indicó que la declinación de abejas y los eventos de extinción de plantas podrían ocurrir cuando sólo el 25% de la población forrajera muestra daños cognitivos. Los porcentajes más altos de daños cognitivos mostraron 50% de pérdida de abejas en sólo cinco temporadas virtuales y eventos de extinción en todo el sistema en <20 temporadas virtuales bajo algunas condiciones. La extinción de las especies de plantas ocurrió sin importar el tamaño poblacional de las abejas, lo que indica que los cambios inducidos por los estresantes tan sólo al comportamiento polinizador podrían resultar en la pérdida de especies dentro de las comunidades botánicas. Estos resultados indican que los efectos estresantes subletras en los mecanismos de comportamiento de los polinizadores, aunque parezcan insensificantes a nivel de individuo, tienen el potencial acumulativo, en principio, de degradar las interacciones entre especies de plantas y polinizadores a nivel de sistema. Nuestro trabajo resalta la importancia de una estrategia de modelado basado en el agente para la identificación y mitigación de los impactos antropogénicos sobre los sistemas planta-polinizador.

PALABRAS CLAVE:
abejo, búsqueda de alimento, comportamiento, interacciones planta-polinizador, memoria, modelo basado en el agente, simulación, transferencia de polen

模拟人类影响对传粉者个体行为到传粉系统的尺度放大
摘要理解人为干扰如何影响植物-传粉者系统对于保护生物多样性和生态系统功能具有重要意义。以往的实验室研究表明，农药使用和病原体是近年来全球传粉者数量急剧下降的主要原因，且会影响传粉者适应性利用资源库和有效传粉的行为过程。然而，目前尚不清楚这些亚致死胁迫在个体水平上对传粉者-植物相互作用的影响是否有潜力通过尺度放大来影响系统水平上野生植物和传粉者的种群动态。我们开发了一个经验参数化的基于主体的模型来模拟大黄蜂传粉者系统 (SimBee)，并测试了 20 多个模拟季节中，胁迫引起的个体觅食者记忆能力和信息处理速度下降对蜜蜂丰度情景 1)、植物多样性情景 2) 和蜜蜂-植物系统稳定性情景 3) 的影响。对大黄蜂和四种同花传粉植物的简单传粉网络建模表明，当 25% 的觅食种群出现障碍障碍时，就可能产生传粉数量减少和植物物种灭绝事件。在某些情况下，较高的感知障碍率会导致仅在 5 个模拟季节内蜜蜂种群就丧失 50%，在小于 20 个模拟季节内发生系统范围内的灭绝事件。植物的灭绝与蜜蜂种群大小无关，这表明仅仅是胁迫引起的传粉者行为变化就可能导致植物种群中物种的消失。以上结果表明，亚致死胁迫对传粉者行为机制的影响虽然在个体水平上不显著，但在系统水平上具有降低植物-传粉者相互作用的累积效应。本研究凸显了基于主体的建模方法对于识别和减轻人类活动对植物传粉系统影响研究的重要性。【翻译：胡怡思；审校：徐永刚】

关键词: 大黄蜂, 记忆, 行为, 植, 传粉者相互作用, 基于主体的模型, 觅食, 花粉转移, 模拟

INTRODUCTION
Over the past decade, wild pollinators have declined in abundance, species richness, and geographic distribution at an alarming rate worldwide (Cameron et al., 2011; Goulson et al., 2015). Although the cause of these declines is unknown, human-introduced stressors such as pesticides, disease, habitat loss, and climate change have all been identified as potential contributing factors (Goulson et al., 2008). Given that many wildlife species depend on animal-pollinated plants for food, shelter, and nesting habitat, pollinator loss has the potential to significantly degrade the function and diversity of terrestrial
ecosystems. Indeed, abundance and diversity of flowering plants have declined in parallel with their pollinators in many locations (Biesmeijer et al., 2006), suggesting that these cascading negative effects might be well underway. A critical step in the conservation and restoration of wild pollination systems is understanding how anthropogenic stressors affect the dynamics of plant–pollinator interactions over different levels of biological organization and over ecologically relevant temporal scales. However, such data are often difficult to obtain due to the significant logistical challenges associated with conducting long-term controlled experimental studies of natural systems (Becher et al., 2013; Henry et al., 2017).

Agent-based modeling (ABM) is a powerful and widely used tool for studying complex natural biological systems (Grimm & Berger, 2016; Stillman et al., 2015), such as those involving plants and pollinators (Becher et al., 2013; Crone & Williams, 2016; Olsson et al., 2015; Qu et al., 2013). Unlike traditional analytically formulated models, ABMs enable the development of a virtual system in which multiple unique and autonomous entities (virtual individuals known as agents) interact with each other and their environment as they do in the real system, thereby providing greater insight into how different factors act singly or together to cause different system states in the wild (Stillman et al., 2015). These models thus allow for investigation of how individual variation in a particular trait or behavior scales up to influence processes at higher levels of biological organization. Importantly, observed system patterns should emerge naturally from the interactions of individuals rather than being explicitly encoded by the simulation. The use of ABMs can be informative for wildlife conservation and management (Allen et al., 2016; McLane et al., 2011; Tracey et al., 2014). For example, Nabe-Nielsen et al. (2018) used an ABM approach to test whether collective changes to individual movement patterns and foraging decisions caused by noise from wind farm construction had the potential to drive decline in North Sea porpoise (Phocaena phocaena) populations.

We used an ABM approach to investigate the potential for sublethal stressor effects on individual pollinators to act as drivers of population decline and loss of species diversity in pollinator–plant networks. Previous work has established that sublethal exposure to pesticides and pathogenic organisms impairs cognitive functioning and decreases foraging success in bee pollinators (Gegear et al., 2006; Otterstatter et al., 2005; Riddell & Mallon, 2006; Siviter et al., 2018; Wright et al., 2015). For example, Stanley et al. (2015) showed that 50% of bumblebees (B. terrestris) could not remember the reward properties of available flowers 24 hr after chronic exposure to a field-realistic dose of a neonicotinoid pesticide. In another bumblebee species (B. impatiens), Mobley and Gegear (2018) found that individuals with an activated immune system took 40% longer to make foraging decisions than controls, significantly reducing the rate of reward delivery to the colony. However, it is unclear whether or not stressor effects observed under highly controlled laboratory conditions would be sufficient to drive the rapid and widespread decline of bee populations in the wild. Moreover, bee foraging decisions have important consequences for plant reproductive success because they mediate pollination efficiency, yet little is known about how stressor-induced changes to bee foraging behavior influence the structure and stability of plant communities.

To fill these knowledge gaps, we created an ABM of a bumblebee pollination system, hereafter referred to as SimBee. The model is parameterized based on data provided in previous field and laboratory experiments on bumblebees and bumblebee-pollinated plants at the individual level (Appendix S1). Although these parameters are realistic values, the purpose of SimBee is to demonstrate and provide a mechanistic understanding of how sublethal stressor effects at the individual level affect processes at the population and community level, rather than to make precise numerical predictions. This distinction of the model purpose is particularly important to policy makers (Grimm, Johnstone, et al., 2020). Although previous ABMs were developed to examine effects of human-introduced stressors on either pollinator (Becher et al., 2014, 2018) or plant (Qu et al., 2013) populations alone, our model allows for plant and pollinator populations to fluctuate freely in response to one another over time, thereby enabling further assessment of how such stressor effects influence system dynamics.

METHODS

Model overview

We used the NetLogo platform (Wilensky, 1999) to create SimBee, a virtual bumblebee pollination system. Individual virtual bees store floral reward information about different plant species in working memory. Bees use this information to adaptively and rapidly collect resources for the colony (bee fitness) under highly variable floral resource conditions, transferring pollen among four co-flowering plant species in the process (plant fitness) over multiple virtual seasons. Bee–flower interactions at the individual level thus dictate the population dynamics and diversity of the system. Primary entities (bees, plants, and colonies) and processes of SimBee are described below and shown in Figure 1. Full details of SimBee are provided in Appendix S1, following the ODD protocol (Grimm et al., 2006, 2010; Grimm, Railsback, et al., 2020), including references for parameterization of the model. See Appendix S3 for model code.

Bees

Bees move through the virtual environment visiting and collecting rewards from flowers in consecutive field of views (FOVs) (approximately 0.096% of the simulated foraging environment). For each virtual season, bees begin in sampling mode, where they randomly visit one flower of each plant species present in each FOV. Bees update their memory by storing the floral reward collected and plant species identity for each visit (memory capacity = 10 reward–species pairs). Bees next enter foraging mode and visit what they decide is the most rewarding flower species in each FOV. The probability of a visit is based on the average reward values for each plant species in memory (details of the decision-making algorithm in Appendix S1). As bees forage, information is updated in memory. Once
FIGURE 1  Primary entities and processes of the SimBee system (red shading in green diamond, bee field-of-view [FOV]; sampling mode, bees randomly visit one flower of each plant species present in each FOV; foraging mode, bees visit the most rewarding flower species in each FOV). Number of new bees and plants based on reward gathered and number of seeds produced during a virtual season, respectively.

capacity is reached, each new value pair replaces the oldest pair. Bees alternate between sampling and foraging modes for the rest of the virtual season (5% sampling mode, 95% foraging mode). Each bee collects 80 units of nectar reward per foraging bout and deposits all rewards (nectar and pollen) in the colony between bouts. Total reward in the colony at the end of the season determines the size of the bee population the following virtual season, unless bee populations are held constant. Bees with impaired memory capacity fail to store information in memory; therefore, they randomly select one flower from each FOV to visit. Bees with decreased information processing speed take 40% longer per flower visit.

Plants

Reward levels of each virtual plant species follow a uniform distribution bounded by a specified minimum and maximum value. Upon bee arrival at the flower, reward is replenished with an amount randomly drawn from the distribution; thus, each plant has a floral reward that varies around the fixed average reward for that species. Bees pick up 40 grains of pollen per flower visit and deposit them during subsequent flower visits following the exponential decay function in Rademaker et al. (1997). Each plant has the potential to produce one seed per bee visit up to a maximum of six seeds per plant. Deposition of conspecific pollen results in the production of a seed (pollination), whereas deposition of heterospecific pollen results in the elimination of an empty seed slot (stigma blockage). The probability of a pollination event is equal to the proportion of the conspecific pollen carried by the bee when it lands on the flower. At the end of each virtual season, a random selection of 40% of total seeds produced by plants determines population size for each plant species during the next virtual season, unless plant populations are held constant.

Model design assumptions

The SimBee system was designed to include only elements essential to address our central question of whether stressor-induced changes to forager behavior can scale up from the individual to the system level. Consequently, we did not include known lethal and sublethal stressor effects on other aspects of the bumblebee life cycle, which would only increase deleterious effects on our bee–plant system. We abstracted the critical features of individual bee–plant interactions into key model processes governing forager behavior, memory, decision-making, and pollen transfer. The most important design concept in the model is the ability of foragers to use memory to adapt their behavior to maximize fitness in a varying floral environment. We assumed that bees remember receiving floral rewards from each plant species in the past, but rely on information stored in working memory to obtain and act on current average reward values associated with each species. Although our virtual season does not currently include natural seasonal effects, such as floral blooms, it does allow for testing of different kinds of variation in floral environments that might arise during a real-world season, such as equal or unequal average floral rewards and plant species abundances.

We also assumed that sublethal stressor effects influence individual bee–plant interactions over the entire virtual season and between virtual seasons. We believe this is a reasonable assumption because nectar and pollen contaminated with pesti-
of cognitively impaired individuals, which reflects the range of frequencies of impaired individuals in previous studies on sublethal effects of pesticide and pathogen exposure on bumblebees. Each type of cognitive impairment was tested separately for each scenario. The starting populations were 100 bumblebees and either 4000 (scenario 1) or 1000 (scenarios 2 and 3) individuals of each plant species. For each experiment, we ran 100 replicates over 20 virtual seasons. Specific model variable settings used in each scenario are provided in Appendix S1.

System patterns in the SimBee model

To consider our model realistic enough for its purpose, we confirmed that emergent patterns resulting from individual bee–plant interactions matched those present in natural systems (Appendix S2). Virtual bees used floral reward information stored in memory to make foraging decisions that were adaptive for the colony (Appendix S2). Bee foraging (pollen transfer) patterns had a direct effect on plant reproductive success. In addition, we found that virtual bees with normal memory exhibited floral constancy, just as real bees do (Waser, 1986), making like–like floral moves in more than half of their floral visits, even when all four floral species were equally rewarding. In contrast, bees lacking memory visited floral species at random, with a consequent reduction in seed production (Appendix S2). Thus, plant reproductive success depended as expected on bee foraging behavior.

Experimental scenarios

We investigated effects of stressor-induced changes to bee cognition and foraging behavior on bee abundance and plant diversity under three ecologically relevant model scenarios (Table 1). The degree of each type of cognitive or behavioral impairment in foragers was based on previous laboratory work (Gegear et al., 2006; Riddell & Mallon, 2006; see references in Moby & Gegear, 2018; Siviter et al., 2018) and included either an inability to remember the reward properties of available flowers (decreased memory capacity) or a 40% delay in the amount of time required to process information (decreased information processing speed). For each experiment within a scenario, forager populations contained 0%, 25%, 50%, 75%, or 100% of cognitively impaired individuals, which reflects the range of frequencies of impaired individuals in previous studies on sublethal effects of pesticide and pathogen exposure on bumblebees. Each type of cognitive impairment was tested separately for each scenario. The starting populations were 100 bumblebees and either 4000 (scenario 1) or 1000 (scenarios 2 and 3) individuals of each plant species. For each experiment, we ran 100 replicates over 20 virtual seasons. Specific model variable settings used in each scenario are provided in Appendix S1.

Effects on bee abundance only (Scenario 1)

We tested for sublethal stressor effects on bee populations when plant abundance and diversity were held constant (Table 1, bee abundance scenario). This scenario simulated an ecological condition in which bee foraging decisions had a minimal influence on the persistence of plant populations. Each plant species was assigned a different mean reward level so that foragers specializing on the species with the greatest mean reward maximized reward intake by the colony.

Effects on plant diversity only (Scenario 2)

We tested for sublethal stressor effects on plant diversity when bee (pollinator) abundance was held constant (Table 1, plant diversity scenario). This scenario simulated an ecological condition in which stressor exposure altered bee foraging behavior, but not to an extent that reduced bee abundance. Plant population size in this scenario depended directly on the foraging decisions of bees (i.e., degree of conspecific and heterospecific pollen transfer). To allow increases in plant numbers over time and persistence of all plant species, we reduced initial plant population sizes and assigned the same mean (min, max) floral reward level to all species.

Effects on system stability (Scenario 3)

We tested for sublethal stressor effects on the integrity of the entire system by allowing bee and plant populations to change over time in response to one another (Table 1, system stability scenario). This scenario simulated an ecological condition
FIGURE 2 Model simulations of sublethal stressor effects on bee population size with constant plant abundance and diversity (scenario 1). Mean (SD) number of bees in the system over 20 virtual seasons under decreasing (a) memory capacity and (b) processing speed (impaired, cognitive impairment; error bars, SD). One hundred simulations were run for each experimental condition.

RESULTS

Simulated effects of sublethal stressors on bee abundance (Scenario 1)

Under the control condition (0% impaired bees), bee population size increased slightly over 20 virtual seasons when plant populations were held constant (Figure 2). Bee population decline was observed when even 25% of the forager population had decreased memory capacity (Figure 2a) or decreased processing speed (Figure 2b), and the rate and magnitude of decline increased with an increase in the percentage of impaired individuals in the foraging population. For example, population decreases for bees with impaired memory capacity ranged from 26% (25% impaired) to 73% (100% impaired) after 10 virtual seasons. Slightly greater declines were observed when a percentage of bees had decreased processing speed; population decreases ranged from 33% (25% impairment) to 83% (100% impairment) over the same period.

Simulated effects of sublethal stressors on plant diversity (Scenario 2)

Under control conditions, a constant forager population of 100 unimpaired individuals maintained populations of all four plant species for 20 generations (Figure 3). Plant diversity decreased as the percentage of the bee pollinator population with decreased memory capacity increased (Figure 3a) due to increases in interspecific pollen transfer. Pollinator population impairment frequencies of 75% and 100% had the greatest effect on plant diversity over 20 virtual seasons and drove the complete loss of three out of four plant species for most simulation runs. The particular plant species lost was random because mean floral reward was the same for all species. Species loss resulted from small differences in plant species populations that arose stochastically and were amplified when impaired bees visited species at random over multiple virtual seasons. Thus, temporally, the dynamics of plant diversity loss followed a sigmoidal rather than linear function for all levels of bee impairment; all four plant species were maintained for the first six virtual seasons followed by a period of rapid species loss in the subsequent seven virtual seasons. In contrast, reductions in processing speed had a minimal effect on plant diversity (Figure 3b). The probability of losing a plant species in a mixed plant community therefore differed depending on the type and frequency of behavioral change in the pollinator population.

Simulated effects of sublethal stressors on system stability (Scenario 3)

Under the control condition over 20 virtual seasons (0% of bees impaired), bee abundance increased, plant populations reached system carrying capacity, and plant diversity was maintained (Figure 4). For sublethal stressors affecting memory capacity (Figure 4a–c), bee and plant populations increased for all but the experiments with 100% impaired bees. However, as the proportion of impaired bees increased, so did heterospecific pollen transfer, resulting in reduced seed set and the eventual loss of plant species (Figure 4c). Under the 50% impaired condition, heterospecific pollen transfer increases alone were sufficient to drive the loss of at least one plant species in the 20 virtual seasons; most simulation runs showed a loss of two species. Loss of one or more species gave other species a better chance to be correctly pollinated by chance by memory-impaired bees; thus, overall plant population levels often reached the carrying capacity of the system, but with much less species diversity. Under 75% and 100% bee impairment conditions, all simulation runs ended with either a single plant species or complete system collapse.

For sublethal stressors decreasing information processing speed (Figure 4d–f), bee population size increased at a slower rate relative to the control at impairment frequencies of 25%, and effects on plant abundance and diversity were small. However, bee abundance decreased in the 50% impaired condition (Figure 4d), causing a corresponding decrease in plant populations and a loss of plant diversity (Figures 4e and 4f) over time.
FIGURE 3  Model simulations of sublethal stressor effects on plant diversity with constant bee population size (scenario 2). Proportion of simulation runs with 4, 3, 2, 1, or 0 plant species remaining at the end of each season: 0–100% of the bee population with (a) decreased memory capacity and (b) decreased processing speed. One hundred simulations were run for each experimental condition.
FIGURE 4  Model simulations of sublethal stressor effects on bee–plant population dynamics (scenario 3). Mean (SD) of (a) number of bees and (b) number of rewarding flowers in the system over 20 seasons under decreasing memory capacity; (c) proportion of simulation runs with 4, 3, 2, 1, or 0 plant species after 20 seasons under decreasing memory capacity; (d) mean (SD) number of bees and (e) rewarding flowers in the system over 20 seasons under decreasing processing speed; and (f) proportion of simulation runs with 4, 3, 2, 1, or 0 plant species remaining at the end of 20 seasons under decreasing processing speed. (One hundred simulation runs for each experimental condition; carrying capacity, 25,921 plants [which provided an upper bound on bee abundance]). Test populations contained 0%, 25%, 50%, 75%, or 100% of foragers with cognitive impairment.

Thus, unlike experimental runs involving decreased memory capacity, plant species declined due to the lack of bee pollinators in the system (pollen limitation) rather than reduced pollen transfer efficiency. Such negative feedback effects were much greater in the 75% and 100% impairment conditions and led to the eventual crash of the entire system in some simulation runs.

DISCUSSION

Pollinator foraging decisions play an important role in maintaining the integrity of pollination systems. Past studies have shown that acute and sublethal exposure to a wide range of pesticides can impair the ability of pollinators to make adaptive decisions (Siviter et al., 2018). However, the vast majority of these studies have been on restrained individuals in a laboratory setting (e.g., the proboscis extension reflex paradigm), making the conservation implications of sublethal pesticide effects on plant-pollinator dynamics in the wild difficult to ascertain. Similarly, there is substantial evidence that pathogenic infection can impair pollinator decision-making (Riddell & Mallon, 2006) and in doing so reduce colony resource acquisition by increasing the amount of time required for foragers to process floral information (Gegear et al., 2006; Mobley & Gegear, 2018). Using an ABM approach, we found that sublethal effects on pollinator decision-making processes at the magnitude and exposure frequency reported in these previous studies have the potential to scale up and drive the decline and loss of bee species from plant–pollinator systems. Because our model is of a simplified pollination system, we cannot use it to make numerically precise predictions; however, our results are consistent with time frames for declines reported for natural pollinator populations. In
addition, our study is the first, to our knowledge, to demonstrate that anthropogenic impacts on pollinator decision-making have the potential to drive the loss of species from plant communities without a parallel decrease in pollinator abundance.

Bee population effects

Our simulations indicated that the impact of decreased memory capacity and information processing speed of bumblebee foragers on rates of population decline varied with the proportion of affected individuals in the population and with floral resource conditions. For example, forager memory impairment caused populations to decline rapidly when average reward level differed among available plant species (scenario 1), but population numbers actually increased when reward level was the same among species (scenario 3) at forager impairment prevalence of 75% or less. This finding was not unexpected, given that memory provided foragers with a clear adaptive advantage in scenario 1 (colony reward intake was greatest when foragers specialized on the most rewarding flowers) but not in scenario 3 (random foraging yielded the greatest energetic return). Decreased memory capacity did, however, drive bee decline in scenario 3 under the 100% forager impairment condition due to the increase in heterospecific pollen transfer, which drove the decline and eventual loss of plant species (floral resource availability). In contrast, decreased information processing speed (i.e., longer decision and flower-handling times) drove bee decline under both floral resource conditions. Thus, sublethal stressors could drive bee population decline in foraging habitats where memory demands are low or even absent, such as agricultural and urban landscapes dominated by a single plant species, if anthropogenic stressors with effects on information processing speed are present. Given that pesticides (Goulson, 2013) and pathogens (Colla et al., 2006; Gillespie, 2010) known to impair bee cognition are both present in such landscapes, this is a reasonable possibility.

Our findings, in combination with the results of previous studies, indicated that sublethal stressor effects on bee cognition and behavior pose a significant threat to the abundance and diversity of wild bees. Past studies have shown that infection rates in wild bumblebees can be as high as 82% for naturally occurring pathogens such as *Crithidia bombi* (Gillespie, 2010) and as high as 40% for non-native pathogens such as *Nosema ceranae* (Dolezal et al., 2016). Studies of wild bee populations in agricultural areas also show sublethal concentrations of insecticides such as clothianidin, thiamethoxam, and bifenthrin in 24–46% of individuals (Hladik et al., 2018). Our model represents a closed ecosystem with a simplified virtual season; thus, exact predictions of expected rate of decline for a particular species in the real world were not possible. However, the model predicted that cognitively impaired foragers at these frequencies would cause a 50% reduction in bee abundance in 4–6 years, which is consistent with declines reported for the endangered rusty patched bumblebee (*Bombus affinis*) and other bumblebee species at risk in North America (Cameron et al., 2011). It is important to note that we used cognitive impairments based on data for a limited number of common, managed bumblebee species (*B. impatiens* and *B. terrestris*), which are likely to be less sensitive to sublethal stressors than wild species at risk. More comparative data on how the magnitude of stressor-induced decreases in cognitive performance varies among bumblebee species are needed to test this possibility. The incorporation of multispecies data on stressor-induced behavioral changes into our model could also be used to investigate how anthropogenic disturbances alter competition in pollinator communities, ultimately causing loss of some species and dominance of others (Banaszak-Cibicka & Zmihorski, 2012). Further development of our model to investigate how other forms of anthropogenic disturbance, such as habitat modification and fragmentation, affect the foraging success of bees and other pollinators could also accelerate conservation efforts to identify, protect, and restore threatened species.

Plant community effects

In addition to driving pollinator decline, our results showed that changes to pollinator behavior caused by stressor-induced cognitive impairment could have profound negative effects on the structure and diversity of flowering plant communities by affecting either the quality or quantity of pollen transferred among individual plants. In scenarios 2 and 3 under control conditions, populations of all four plant species were stable over 20 virtual seasons because individual bees exhibited floral constancy (i.e., individual foragers temporarily specialize on flowers of one plant species despite the availability of equally rewarding flowers of other plant species [Waser, 1986]). Flower constancy increases plant reproductive success by reducing heterospecific pollen transfer.

Our results indicated that even a marginal stressor-induced decrease in flower constancy due to impairment of memory capacity was sufficient to cause the decline and loss of species from plant communities in scenarios 2 and 3 (Figures 3a and 4a–c). In contrast, a decrease in information processing speed had no effect on bee constancy levels and therefore had no effect on plant abundance and diversity in scenario 2 (Figure 3b). Decreased processing speed resulted in plant species loss in scenario 3 (Figure 4d–1); however, it was driven by the decline of bee populations (pollen quantity) rather than flower constancy (pollen quality). Previous modeling approaches to plant species extinctions in pollination networks were based on the assumption that pollinator loss is necessary to initiate plant extinction events (Traveset et al., 2017; Vieira & Almeida-Neto, 2015). However, we found that changes to pollinator behavior alone could cause the loss of plant species even when pollinator populations remained stable (Figure 3a) or even increased over time (Figure 4a–c). In fact, we found behaviorally driven single and multiple species extinction events in plants occurred in as few as seven virtual seasons and coextinction events (bees and plants) occurred in as few as nine virtual seasons.

Based on these results, we expect the greatest risk of plant extinction due to changes in pollinator behavior to occur in mixed plant communities containing species with high levels
of pollinator specificity, reproductive dependence on animal pollination, and demographic dependence on seed production (Bond et al., 1994). From the perspective of biodiversity conservation, changes to pollinator behavior resulting in reduced pollination efficiency can negatively affect secondary wildlife consumers through reductions in the availability of seeds and fruit even when plant species have a low dependence on pollinators or can compensate for decreased seed production (Newton, 2004; Titulaer et al., 2017). Interestingly, when plant species diversity in our model dropped to just one or two species due to memory capacity impairment, populations of bees and those plant species began to increase because of the reduced chance of heterospecific pollen transfer. Thus, pollinator behavior can provide a better proxy for plant extinction risk than pollinator abundance in some cases and therefore must be considered when developing effective conservation and management strategies for threatened pollination systems.

**ABM and the conservation of plant–pollinator systems**

Our findings highlight the importance of using an ABM approach to understand how anthropogenic disturbance influences the structure and dynamics of pollination networks through changes to pollinator behavior. Mathematical network models often use the degree of interactions among species to predict extinction scenarios (Landi et al., 2018). However, it is well documented that the behavior of individuals within a species is often far more specialized than the average behavior over the population (Tur et al., 2014). For example, flower constancy in bumblebees is observed at the level of individuals, even in generalist species (Gegear & Laverty, 2005; Goulson, 1999). In our virtual system, flower constancy was an emergent property resulting from interactions between memory limitations in bees and floral resource variability among plants. Failing to account for the behavior of individuals can result in underestimates of the likelihood of extinction of a species (Ellner et al., 2020; Morán-López et al., 2020). More recent stochastic extinction models recognize that interaction strengths can vary and that plant–pollinator mutualisms are more important in predicting species loss than interaction strength alone (Traveset et al., 2017; Vieira & Almeida-Neto, 2015). Although network models have become increasingly complex and small scale, they still lack the fundamental individual mechanisms that determine the tipping points between population persistence and decline (DeAngelis & Grimm, 2014). However, network models include data that are critically relevant to extinction prediction. In fact, inclusion of field data on variation in floral preference among bumblebee species and mating strategies among plant species in natural systems, as well as seasonal variations in pollinator and plant populations, will be an important future step toward improving the ability of our model to predict the long-term effects of anthropogenic disturbance on biodiversity and ecosystem health.

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**LITERATURE CITED**

Allen, C. H., Parrott, L., & Kyle, C. (2016). An individual-based modelling approach to estimate landscape connectivity for big-horn sheep (Ovis canadensis). PeerJ, 4, e2001.

Banaszak-Gibicka, W., & Zmińcziński, M. (2012). Wild bees along an urban gradient: Winners and losers. Journal of Insect Conservation, 16, 331–343.

Becher, M. A., Grimm, V., Thorbek, P., Horn, J., Kennedy, P. J., & Osborne, J. L. (2014). BEEHAVE: A systems model of honeybee colony dynamics and foraging to explore multifactorial causes of colony failure. Journal of Applied Ecology, 51, 470–482.

Becher, M. A., Osborne, J. L., Thorbek, P., Kennedy, P. J., & Grimm, V. (2013). REVIEW: Towards a systems approach for understanding honeybee decline: A stocktaking and synthesis of existing models. Journal of Applied Ecology, 50, 868–880.

Becher, M. A., Twiston-Davies, G., Penny, T. D., Goulson, D., Rotheray, E. L., & Osborne, J. L. (2018). Bumble-BEEHAVE: A systems model for exploring multifactorial causes of bee decline at individual, colony, population and community level. Journal of Applied Ecology, 55, 2790–2801

Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Oehlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., & Settele, J., Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science, 313, 351–354.

Bond, W. J., Lawton, J. H., & May, R. M. (1994). Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 344, 83–90.

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. Proceedings of the National Academy of Sciences, 108, 662–667.

Colla, S. R., Otterstatter, M. C., Gegear, R. J., & Thomson, J. D. (2006). Flight of the bumble bee: Pathogen spillover from commercial to wild populations. Biological Conservation, 129, 461–467.

Crone, E. E., & Williams, N. M. (2016). Bumble bee colony dynamics: Quantifying the importance of land use and floral resources for colony growth and queen production. Ecology Letters, 19, 460–468.

DeAngelis, D. L., & Grimm, V. (2014). Individual-based models in ecology after four decades. F1000Prime Reports, 6, 39.

Dolezal, A. G., Hendrix, S. D., Seavo, N. A., Carrillo-Tripp, J., Harris, M. A., Wheeldon, M. J., O’Neal, M. E., & Toth, A. L. (2016). Honey bee viruses in wild bees: Viral prevalence, loads, and experimental inoculation. PLoS One, 11, e0166190.

Ellner, S. P., Ng, W. H., & Myers, C. R. (2020). Individual specialization and multitrophic interactions: Disease spread in plant-pollinator networks. The American Naturalist, 195, E118–E1310.

Folly, A. J., Koch, H., Stevenson, P. C., & Brown, M. J. F. (2017). Larvae act as a transient transmission hub for the prevalent bumblebee parasite Crithidia bombi. Journal of Invertebrate Pathology, 148, 81–85.

Gegear, R. J., & Laverty, T. M. (2005). Flower constancy in bumblebees: A test of the trait variability hypothesis. Animal Behaviour, 69, 939–949.
Geiger, R. J., Otterstatter, M. C., & Thomson, J. D. (2006). Bumble-bee foragers infected by a gut parasite have an impaired ability to utilize floral information. *Proceedings of the Royal Society of London B: Biological Sciences, 273*, 1073–1078.

Gillespie, S. (2010). Factors affecting parasite prevalence among wild bumblebees. *Ecological Entomology, 35*, 737–747.

Goulson, D. (1999). Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics, 2*, 185–209.

Goulson, D. (2013). REVIEW: An overview of the environmental risks posed by neonicotinoid insecticides. *Journal of Applied Ecology, 50*, 977–987.

Goulson, D. (2015). Neonicotinoids impact bumblebee colony fitness in the field: A reanalysis of the UK’s Food & Environment Research Agency 2012 experiment. *PeerJ, 3*, e854.

Goulson, D., Lye, G. C., & Darvill, B. (2008). Decline and conservation of bumble bees. *Annual Review of Entomology, 53*, 191–208.

Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science, 347*, 1255957.

Grinn, V., Berger, U., Bastiansen, F., Ellassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S. K., Huse, G., Huth, A., Jepsen, J. U., Jorgensen, C., Mooyi, W. M., Müller, B., Pécré, G., Pion, C., Raubsch, S. F., Robbins, A. M., ... DeAngelis, D. L. (2006). A standard protocol for describing individual-based and agent-based models. *Ecological Modelling, 198*, 115–126.

Grinn, V., Raible, S. F., Vincenot, C., Berger, U., Gallagher, C., DeAngelis, D., Edmonds, B., Ge, J., Ginse, J., Groenendijk, J., Johnston, A. S. A., Miles, A., Nabe-Nielsen, J., Polhill, J. G., Radchuk, V., Rohrlander, M.-S., Stillman, R. A., Theile, J., & Ayllon, D. (2020). The ODD protocol for describing agent-based and other simulation models: A second update to improve clarity, replication, and structural realism. *Journal of Artificial Societies and Social Simulation, 23*, 7.

Grinn, V., & Berger, U. (2016). Structural realism, emergence, and predictions in next-generation ecological modelling: Synthesis from a special issue. *Ecological Modelling, 326*, 177–187.

Grinn, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Ginse, J., & Raible, S. F. (2010). The ODD protocol: A review and first update. *Ecological Modelling, 221*, 2760–2768.

Grinn, V., Johnston, A. S. A., Thuille, H.-H., Forbes, V. E., & Thorbek, P. (2020). Three questions to ask before using model outputs for decision support. *Nature Communications, 11*, 4959.

Henry, M., Becher, M. A., Osborne, J. L., Kennedy, P. J., Aupinel, P., Bretagnolle, V., Brun, F., Grimm, V., Horn, J., & Requier, F. (2017). Predictive systems models can help elucidate bee declines driven by multiple combined stressors. *Apidologie, 48*, 328–339.

Hladik, M. L., Main, A. R., & Goulson, D. (2018). Environmental risks and challenges associated with neonicotinoid insecticides. *Environmental Science & Policy, 82*, 3329–3335.

Krupke, C. H., Hunt, G. J., Eitzer, B. D., Andino, G., & Given, K. (2012). Multi-routes of pesticide exposure for honey bees living near agricultural fields. *PLoS One, 7*, e29268.

Landi, P., Minsartvelo, H. O., Brännström, Å., Hui, C., & Dieckmann, U. (2018). Complexity and stability of ecological networks: A review of the theory. *Population Ecology, 60*, 319–345.

McLane, A. J., Semeniuk, C., McDermid, G. J., & Marceau, D. J. (2011). The role of agent-based models in wildlife ecology and management. *Ecological Modelling, 222*, 1544–1556.

Mobley, M. W., & Geiger, R. J. (2018). Immune-cognitive system connectivity reduces bumblebee foraging success in complex multisensory floral environments. *Scientific Reports, 8*, 5953.

Morán-López, T., Espindola, W. D., Vizzachero, B. S., Fontanella, A., Salinas, L., Arana, C., Amico, G., Pizzo, M. A., Carlo, T. A., & Morales, J. M. (2020). Can network metrics predict vulnerability and species roles in bird-dispersed plant communities? Not without behaviour. *Ecology Letters, 23*, 348–358.

Nabe-Nielsen, J., Beest, F. M. v., Grimm, V., Sibly, R. M., Teilmann, J., & Thompson, P. M. (2018). Predicting the impacts of anthropogenic disturbances on marine populations. *Conservation Letters, 11*, e12563.

Newton, I. (2004). The recent declines of farmland bird populations in Britain: An appraisal of causal factors and conservation actions. *Ibis, 146*, 579–600.

Olsson, O., Bolin, A., Smith, H. G., & Lonsdorf, E. V. (2015). Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. *Ecological Modelling, 316*, 133–143.

Otterstatter, M. C., Geiger, R. J., Colla, S. R., & Thomson, J. D. (2005). Effects of parasitic mites and protozoa on the flower constancy and foraging rate of bumble bees. *Behavioral Ecology and Sociobiology, 58*, 383–389.

Qu, H., Seifan, T., Tiellörker, B., & Seifan, M. (2013). A spatially explicit agent-based simulation platform for investigating effects of shared pollination service on ecological communities. *Simulation Modelling Practice and Theory, 37*, 107–124.

Rademaker, M. C. J., De Jong, T. J., & Klinkhamer, P. G. L. (1997). Pollen dynamics of bumble-bee visitation on *Echinium vulgare*. *Functional Ecology, 11*, 554–563.

Riddell, C. E., & Mallon, E. B. (2006). Insect psychoneuroimmunology: Immune response reduces learning in protein starved bumblebees (*Bombus terrestris*). *Brain, Behaviour, and Immunity, 20*, 135–138.

Sivier, H., Koricheva, J., Brown, M. J. F., & Leadbeater, E. (2018). Quantifying the impact of pesticides on learning and memory in bees. *Journal of Applied Ecology, 55*, 2812–2821.

Stanley, D. A., Smith, K. E., & Raine, N. E. (2015). Bumblebee learning and memory is impaired by chronic exposure to a neonicotinoid pesticide. *Scientific Reports, 5*, 16508.

Stillman, R. A., Raible, S. F., Ginse, J., Berger, U., & Grimm, V. (2015). Making predictions in a changing world: The benefits of individual-based ecology. *Biocene, 65*, 140–150.

Titulaer, M., Melgoza-Castillo, A., Panjabi, A. O., Sanchez-Flores, A., Martinez-Guerrero, J. H., Macias-Duarte, A., & Fernandez, J. A. (2017). Molecular analysis of stomach contents reveals important grass seeds in the winter diet of Baird’s and Grasshopper sparrows, two declining grassland bird species. *PLoS One, 12*, e0189695.

Tracey, J. A., Bevins, S. N., VandeWoude, S., & Crooks, K. R. (2014). An agent-based movement model to assess the impact of landscape fragmentation on disease transmission. *Ecosphere, 5*, 1–24.

Traveset, A., Tur, C., & Eguíluz, V. M. (2017). Plant survival and keystone pollinator species in stochastic coextinction models: Role of intrinsic dependence on animal-pollination. *Scientific Reports, 7*, 6915.

Tur, C., Vigalondo, B., Trojelsgaard, K., Olesen, J. M., & Traveset, A. (2014). Downscaling pollen-transport networks to the level of individuals. *Journal of Animal Ecology, 83*, 306–317.

Vieira, M. C., & Almeida-Neto, M. (2015). A simple stochastic model for complex coextinctions in mutualistic networks: Robustness decreases with connectivity. *Ecology Letters, 18*, 144–152.

Waser, N. M. (1986). Flower constancy: Definition, cause, and measurement. *The American Naturalist, 127* (5), 593–603.

Wilensky, U. (1999). *NetLogo*. Center for Connected Learning and Computer-Based Modeling, Northwestern University. http://ccl.northwestern.edu/netlogo/

Wright, G. A., Softley, S., & Earnshaw, H. (2015). Low doses of neonicotinoid pesticides in food rewards impair short-term olfactory memory in foraging honeybees. *Scientific Reports, 5*, 15322.

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