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Communicating across boundaries: an examination of social information use by foraging bees and of integrated assessments in ecology teaching

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An abstract of

A dissertation submitted to the Faculty of the

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Abstract

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In this dissertation, I present research in two disciplines. The first is behavioral ecology. In Chapter 1, I measured bees' foraging activity in the presence of honest, misleading, or absent social cues. In this context, the social cue was the sight of another bee on a flower, a powerful influence on bees' decisions about which flowers to forage on. I found that misleading social cues had a lingering influence on bee foraging choices, even after the cue was removed. This indicates that bees that encounter misleading social cues are more likely to learn the characteristics of a rewarding flower instead of relying on the social cue as a shortcut. In Chapter 2, I expanded that experiment by adding a component of human-driven change when I studied the impact of pesticide exposure on social cue use. I found that bees that were exposed to pesticides did not follow social cues while foraging.

The second discipline is biology education research. For Chapter 3, I used qualitative content analysis to study how instructors that teach ecology assess the connections that students make between ecology and concepts from other disciplines. I identified seven strategies that instructors use to integrate diverse disciplinary concepts in their assessments.

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Table of Contents

Introduction

As pollinators, bees play an essential role in maintaining the reproduction of the plant communities that underlie terrestrial ecosystems. For example, animal pollinators are estimated to be needed for the reproduction of 80-90% of angiosperms (Ollerton et al. 2011). Wild bees are particularly important for crop production (Garibaldi et al. 2013) of crops including apples (Mallinger and Gratton 2015) and watermelon (Garibaldi et al. 2013), among many others. The bumble bee *Bombus impatiens* is wild in much of the United States (Williams et al. 2014) and also managed as a commercial pollinator for tomatoes and many other crops (Morandin et al. 2001).

Bumble bees like *B. impatiens* are also valued by scientists as a model system for researching animal cognition (Leadbeater and Chittka 2007a). These bees learn how to identify and handle rewarding flowers through information they gather through their own trial-and-error, called personal information, and information they gather by observing and copying other bees, called social information (Laland 2004; Kawaguchi et al. 2006; Leadbeater and Chittka 2009; Dunlap et al. 2016). Bees yield insight into the environmental conditions in which learning is adaptive (Leadbeater 2015; Dunlap et al. 2017; Leadbeater and Dawson 2017), how learning can be hindered by anthropogenic elements such as antibiotics (Avila et al. 2022), and what the potential costs are of spending time and energy on learning, such as decreased speed of visiting flowers (Chittka et al. 2003) and even a shorter foraging lifespan (Evans et al. 2017).

Though bees are valued both as pollinators and research subjects, bee populations are declining. For example, in the United States, 23% of the land area of the country experienced bee declines from 2008 to 2013 (Koh et al. 2016). Bee decline is likely caused by a combination of parasites, pesticides, and a lack of flowers for bees to forage on (Goulson et al. 2015). One particular class of pesticides called neonicotinoids are of susbstantial concern both for their widespread use and range of effects on non-target organisms (Goulson 2013; Godfray et al. 2014; Godfray et al. 2015). Neonicotinoids influence bee foraging behavior (Yang et al. 2008; Schneider et al. 2012), even changing the types of plants bees visit (Stanley and Raine 2016) and diminishing their ability to learn how to collect pollen (Whitehorn et al. 2017). However, these sublethal effects of neonicotinoid exposure on bees can be subtle and complex, prompting researchers to call for future studies that assess bees' cognitive function in a broad range of increasingly realistic learning scenarios (Muth and Leonard 2019). In sum, while there is a strong evidence basis to support the claim that neonicotinoids change bee cognition, more research is needed to investigate the conditions under which this change occurs and what the implications are for pollination.

Though scientific research is essential for *understanding* bee decline, ameliorating bee decline requires extensive change in culture and policy (Potts et al. 2016; Smith and Saunders 2016). In order to teach these multiple facets of bee decline, science educators have chosen to approach this topic as both a social and scientific issue. For example, instructors engage students' real-world knowledge by incorporating gardens into lessons (Wells et al. 2021), visiting bee hives (Schönfelder and Bogner 2018), and assigning news articles about the issue (Stanisavljević et al. 2016). However, it is unclear how these lessons about bees fit into broader curricula, since instructors (Pauley et al. 2019) and textbooks (Wyner and DeSalle 2020) both face limitations in integrating content about science and society. The recently developed 4-Dimensional Ecology Education (4DEE) framework calls for such integrated lessons (Berkowitz et al. 2018), though it is unclear how instructors should approach this integration.

The research reported in this dissertation addresses the overlap between social and ecological issues in two different ways. First, through behavioral ecology research, I sought to better understand bee cognition during foraging. Specifically, in Chapter 1, I present a study in which I investigated how social information, such as the sight of another bee on a flower, influences bees' foraging choices. For Chapter 2, I studied how neonicotinoid exposure changes those patterns of social cue use. My second approach in researching social and ecological issues was to conduct biology education research to examine how these issues are taught. Specifically, in Chapter 3, I describe a study in which I examined how college-level ecology instructors incorporate information from multiple dimensions of the 4DEE framework in their assessments. Although bee decline is only one topic that might come up in an ecology course, understanding how instructors prepare students to make sense of topics that span ecology and other disciplines is an important step toward learning how to make cultural, social, and political changes that can ameliorate the loss of pollinator populations.

For Chapter 1, I investigated how training with social cues influenced bee foraging choices the next day, when the social cues were removed. While existing literature shows that social cues have a powerful influence on bees' foraging choices, it is unclear how temporary social cues influence bees' future foraging trips. I used experiments in a laboratory artificial foraging arena to address this gap. In the foraging area, I was able to isolate the study factors I was most interested in (particularly social cues) while maintaining controlled conditions that would not be possible in a field study. I evaluated bees' foraging activity over two days, comparing the behavior of bees that were trained with honest, misleading, or no social cues. I measured the extent to which bees preferred a rewarding, blue flower on Day 1, while social cues were present, and on Day 2, when social cues were absent and the blue flower was no longer more rewarding than an alternative. While this study yielded insight into bee foraging behavior, I built on this work to next add a greater degree of field realism by investigating how this system is affected by an element of anthropogenic change.

In Chapter 2, I present a study of the effect of neonicotinoid pesticides on social cue use. Since neonicotinoids can impact bee cognition, I evaluated whether pesticide exposure would cause bees to rely more heavily on social cues rather than their own personal information acquired through trial-and-error. To test the influence of pesticide exposure on bee social cue use, I again used the laboratory foraging arena to measure bees' responses to honest, misleading, and no social cues. However, this experiment measured foraging only while cues were present (with the exception of the no-cue control) and also compared the performance of bees who had and had not been exposed to field-realistic amounts of the neonicotinoid pesticide thiamethoxam. While I believe studying the ecological implications of anthropogenic change is important, for my final chapter I chose to study how these complex ecological patterns are taught at the undergraduate level.

For Chapter 3, I assessed the extent to which instructors integrate ecology with other disciplinary concepts in Ecology course assessments. Specifically, I evaluated how ecology teaching aligns with a recently proposed curriculum framework called 4 Dimensional Ecology Education (4DEE), which calls for ecology lessons that integrate information from other sciences, with research skills, and in the context of human-environment interactions. I used qualitative content analysis of exams and other assessments used in courses that teach ecology to evaluate how professors assess students' ability to integrate ecology concepts with the other 4DEE dimensions. Future studies can build on this research by investigating the impact integrated assessments have on students' academic and career success.

Chapter 1

Misleading social cues have a lingering influence on foraging choices in bumble bees

Abstract

Bumble bees use social cues such as the presence of another bee on a flower to help identify rewarding flowers in a community. Although previous researchers have found that social cues help bees identify flowers, little is known about the potential for lingering effects of social cues on foraging, after the cues are no longer present. To address this gap, we tested whether the reliability of social cues affected bumble bee (*Bombus impatiens*) foraging choices, first while the social cues were present and subsequently one day later, when the social cues were removed. Our hypothesis was that if honest social cues replaced bees' need to learn the characteristics of rewarding flowers, then bees trained with misleading cues would learn those characteristics better than bees trained with honest social cues. In the laboratory, we trained bees to forage on flowers with honest, misleading, or absent social cues. The next day, we tested foraging choices without social cues by measuring preference for a flower that, on Day 1, was more rewarding than an alternative flower but, on Day 2, was as rewarding as the alternative flower. We found that only bees trained with misleading social cues exhibited a preference for the previously rewarding flower the next day, after social cues were removed. This result is consistent with the idea that, instead of just copying others, bees may have weighted their own experience more strongly after training with misleading relative to honest social cues.

Introduction

Foraging is a complex challenge for many animals, particularly when a forager is searching for resources that are spatially and temporally ephemeral. This challenge is particularly apparent for pollinators, given the often rapid turnover in blooming of floral resources. To accomplish this complex foraging, bees need to learn to access the pollen and nectar rewards coming from a community of flowers that changes throughout the season, remember which flowers deliver which rewards, avoid competitors and predators, and bring these rewards back to their colony repeatedly throughout the day.

One strategy for meeting this challenge is to use social cues to discover potentially rewarding flowers (Leadbeater and Chittka 2007b). In this context, social cues can be a passive display of information, such as the presence of a conspecific on a food resource indicating that the resource is likely to be rewarding (Dall et al. 2005). In bumble bees, foragers use these passive social cues, as seen in experiments in which bees preferentially visit a flower after seeing another bumble bee on the flower (Leadbeater and Chittka 2009). Social cues can be quite powerful—bees will continue to visit flowers that are indicated by a social cue, even if the social cue often points to a flower that is not rewarding (Dunlap et al. 2016). The information that is shared between bees in this form of communication is called social information. Bees may learn from social information. In this chapter, we use the term “learning” to mean a change in behavior that occurs with relevant experience, a common definition in behavioral ecology work because it is measurable and useful for studying animal cognition in an ecological context (Barron et al. 2015).

While social cues clearly impact bees’ foraging choices while those cues are present, it is unclear how social cues influence their choices in subsequent foraging trips. One possibility is that, when social cues are present, bees not only follow them but also learn the characteristics of the flower that the social cue indicates is rewarding, so that they can seek out that type of flower in future foraging. In this case, bees would make foraging choices by integrating information from past and current social cues as well as their own personal experience of trying to collect resources from different flowers. Alternatively, social cues might act as a shortcut for bees to identify rewarding flowers without having to learn the characteristics of those flowers. In this case, bees may have adapted to forage on ephemeral floral resources by following social cues only when they are present and not investing energy in making foraging trips that align with old cues.

There is some precedence for the alternative prediction that reliable social information does not influence foraging after social cues are removed because foragers had only learned information about the social cue, not the rewarding resource it led to (Giraldeau et al. 2002). For example, birds may use social cues from conspecifics, observing their conspecifics' discovery of food sites and stealing those food resources (Laland 2004). Previous researchers have found that pigeons who follow social cues to food caches placed by the researchers are not able to find the same food caches on subsequent trips without social cues until they forage by themselves and learn by trial-and-error (Giraldeau and Lefebvre 1987). However, in studies like this where social cues accurately indicate a reward, a forager is not incentivized to learn the characteristics of a rewarding resource while the social cue is present. In nature, not all social cues are accurate; animals also learn from social cues that are misleading and do not directly indicate a reward (Laland and Williams 1998). If bees are misled by social cues to a flower that is not rewarding, it may be more advantageous for those bees to identify an alternative flower that *is* rewarding and learn the rewarding flower's characteristics to distinguish it from the not rewarding flower, in order to avoid being misled in future. Thus, our hypothesis is that bees trained with misleading social cues should learn the characteristics of a rewarding flower, and that information should influence future foraging trips, in that bees would preferentially visit the flower they had learned was rewarding.

Do honest or misleading social cues influence bees' learning about foraging resources and their foraging choices in the future? To address this question, we trained bees to forage in a foraging arena with two flowers, where one flower color was more rewarding than the other. In addition to color, flowers were also distinguished by the presence of social cues. Some of the bees were trained with honest social cues that indicated the more-rewarding flower, some with misleading social cues that indicated the less-rewarding flower, and a control group was trained with no social cues. The next day, we tested them in a scenario with no social cues and with the previously more-rewarding flower and a novel, equally rewarding flower. We hypothesized that if, like scrounging pigeons, bees that copy social cues are using the cue as a shortcut to identify rewarding flowers without learning the characteristics of the flowers themselves, then bees trained with honest social cues *would not* learn to associate flower color with reward, but bees trained with misleading social cues *would* learn to associate flower color with reward and would use this information to choose flowers on future foraging trips.

Methods

Study System

We used four *Bombus impatiens* colonies purchased from Koppert Biological Systems (Howell, Michigan). Colonies were housed in a plastic container (0.600 x 0.416 x 0.165 m) with metal screened sides. Bees that were used in experiments were placed in subcolonies housed in plastic containers (22.2 x 16.8 x 14.0 cm) with metal screened sides that were placed next to the main colony so that they were exposed to queen pheromone and also were easy to access for experiments. Bees continued to live in these subcolonies (next to the main colony) throughout the experiment and were only removed temporarily for trials. All colonies were kept in a dark room. Bees in their colonies and subcolonies were fed ad lib pollen (Koppert Biological Systems, Howell, MI) and 1 M sugar water solution. The same solution was used in the foraging arena.

Table 1: Number of bees used in experiment.

Colony	Social Cue	Number of Bees
1	Control	14
	Honest	8
	Misleading	12
2	Control	18
	Honest	14
	Misleading	20
3	Control	22
	Honest	18
	Misleading	28
4	Control	30
	Honest	32
	Misleading	28

Foraging Arena

Bees were trained and tested over the course of two days in an indoor artificial foraging chamber (0.75 x 2.27 x 0.74m). Bees did not live in the chamber and they did not have continuous access to it. The foraging chamber was divided into seven sub-enclosures (each 42.55 x 30.18 x 17.78 cm) so that we could test multiple bees simultaneously but still have each bee forage alone, since we placed each bee in a different sub-enclosure. Sub-enclosures were opaque white on the sides, to prevent the bees from seeing other bees, and screened in on the top for air flow. Sub-enclosures were thus open to light and heat from the ceiling of the foraging chamber. The ceiling of the foraging chamber was lit with incandescent light bulbs that also heated the chamber to 28ºC. Each sub-enclosure contained two artificial flowers, one of each type as described below (14 total flowers in the chamber).

Flowers were 3D-printed and painted with acrylic paint (Crayola, Forks Township, Pennsylvania), such that they contrasted both in color and shape from the green plastic chamber floor. We chose to train bees to form associations between flower color and reward because previous studies of bee foraging have shown that bees readily form these associations (Gumbert 2000; Kunze and Gumbert 2001; Worden and Papaj 2005; Kaczorowski et al. 2012). These associations between flower color and reward mimic bees' color associations while foraging in the wild (Chittka et al. 1997).

We tracked bee foraging within each sub-enclosure using a Radio Frequency Identification (RFID) system that identified each bee and each flower. To do this, we attached an RFID tag (mic3-TAG RFID tag; 1.9 x 1.6 x 0.5 mm; Microsensys, Gainesville, FL) to each bee one week before trial. We attached the tags with glue (Elmer's Carpenter's Wood Glue) to each bee's thorax. An RFID reader was placed at the entrance to each artificial flower. This RFID reader was triggered when a bee wearing an RFID tag passed next to it, entering a small cavity in the middle of the flower. Once triggered by a bee, an artificial flower dispensed a 3µl droplet of liquid (either artificial nectar or water). The liquid was delivered through pneumatic solenoid valves (Skycraft Surplus, Orlando, Florida) that were controlled by Arduino UNO microcontrollers. All visits to flowers were automatically recorded by the RFID system.

Bees were placed in the foraging chamber sub-enclosures to forage for 30-minute periods (one trial on each of two consecutive days), during which time each bee had access to two flowers. In previous studies of foraging in bees, researchers controlled the amount of exposure to a foraging arena by limiting the number of visits to flowers, instead of limiting foraging time (Gumbert 2000; Dunlap et al. 2016; Evans et al. 2017). A time-based approach was more logistically feasible in our experiment because the bees did not have continuous access to the foraging chamber from their colony, but instead individuals were placed into the chamber sub-enclosures manually before training or testing began. We cleaned the foraging chamber, sub-enclosures, and flowers with a 70% ethanol solution between all trials to remove any potential pathogens or scent marks. We flushed the tubing within the chamber with 1% bleach solution periodically between trials, rinsing well to remove any residual bleach.

Social Cue Conditions

Previous researchers have argued that research on animal cognition should be done in experiments with rigorously consistent cues (Rowe and Healy 2014). In order to consistently define one flower as better than the other on Day 1, we aligned the sensory cues in the same way: all bees were naïve to the foraging chamber and the artificial flowers before the experiment; the rewarding flower was blue, a salient color cue toward which bumble bees exhibit an inherent positive bias, as in they visit that flower more often (Raine et al. 2006); and the reward quantity and type (rewarding or unrewarding) were consistent throughout.

While bees were foraging during training (on the first day of trials), some flowers had a social cue placed on them (Figure 1). The social cue was a dead, frozen, and pinned conspecific from a different colony. Dead conspecifics are commonly used as a social cue in research on foraging in bees (e.g., Worden and Papaj 2005; Kawaguchi et al. 2006). The social cue was placed on the rewarding, blue flower in the "honest social cue" condition. The social cue was placed on the non-rewarding, green flower in the "misleading social cue" condition. Thus, in honest trials, the social cue was aligned with the preferred color of flower and the reward, but in misleading trials, the social cue conflicted with these factors. The social cue was absent in the control condition. On the second day of trials (testing), we did not place social cues on any flowers (Figure 1).

Training- Day 1

Bees' first exposure to the foraging chamber was a training scenario. Before foraging, all bees were placed into 50ml falcon tubes (one bee per tube) and deprived of food for at least two hours (a common technique to enhance foraging, e.g., Rademaker et al. 1997; Manson et al. 2010) Each bee was presented with two flowers, a blue flower that offered a sugar water reward and a green flower that offered only water (neither reward nor punishment). One of the flowers may have had a social cue placed on top of it, as described in the Social Cue Conditions section. Over 30 minutes, we recorded the number of times that each bee collected a reward from a flower after triggering the RFID reader with its RFID tag. After 30 minutes, the bee was removed from the sub-enclosure and chamber. Once bees were removed from the chamber, they were placed back into their subcolony and fed *ad libitum* pollen and nectar.

Test- Day 2

On the day after training, bees were placed in the foraging chamber again in a test scenario. Preceding this trial, all bees were placed in individual tubes and food-deprived for at least two hours as described for Day 1. Once in the chamber, bees were presented with two flowers for 30 minutes: the same, rewarding blue flower and a novel purple flower that was as rewarding as the blue (i.e., both flowers dispensed the same sugar-water solution). We did not use a green flower again, because we wanted to measure the effect of bees' experiences with blue flowers as rewarding independent of their experience with green flowers as not rewarding. We also chose to make the purple flower offer the same reward as the blue flower so that our experiment was not confounded by either the effects of bees learning to prefer blue or purple flowers (whichever would have been more rewarding) during the second-day trials, or the effect of bees learning that neither flower was rewarding and ceasing to forage (if we had made both flowers not rewarding). The position of the blue flower relative to the non-blue flower (either green or purple) was switched between Day 1 and Day 2. No social cues were used on the test day. We recorded the number of visits each bee made to both flowers. We considered a visit to have occurred when a bee landed on a flower, their RFID tag triggered the RFID reader in a flower, and a droplet of nectar was dispensed.

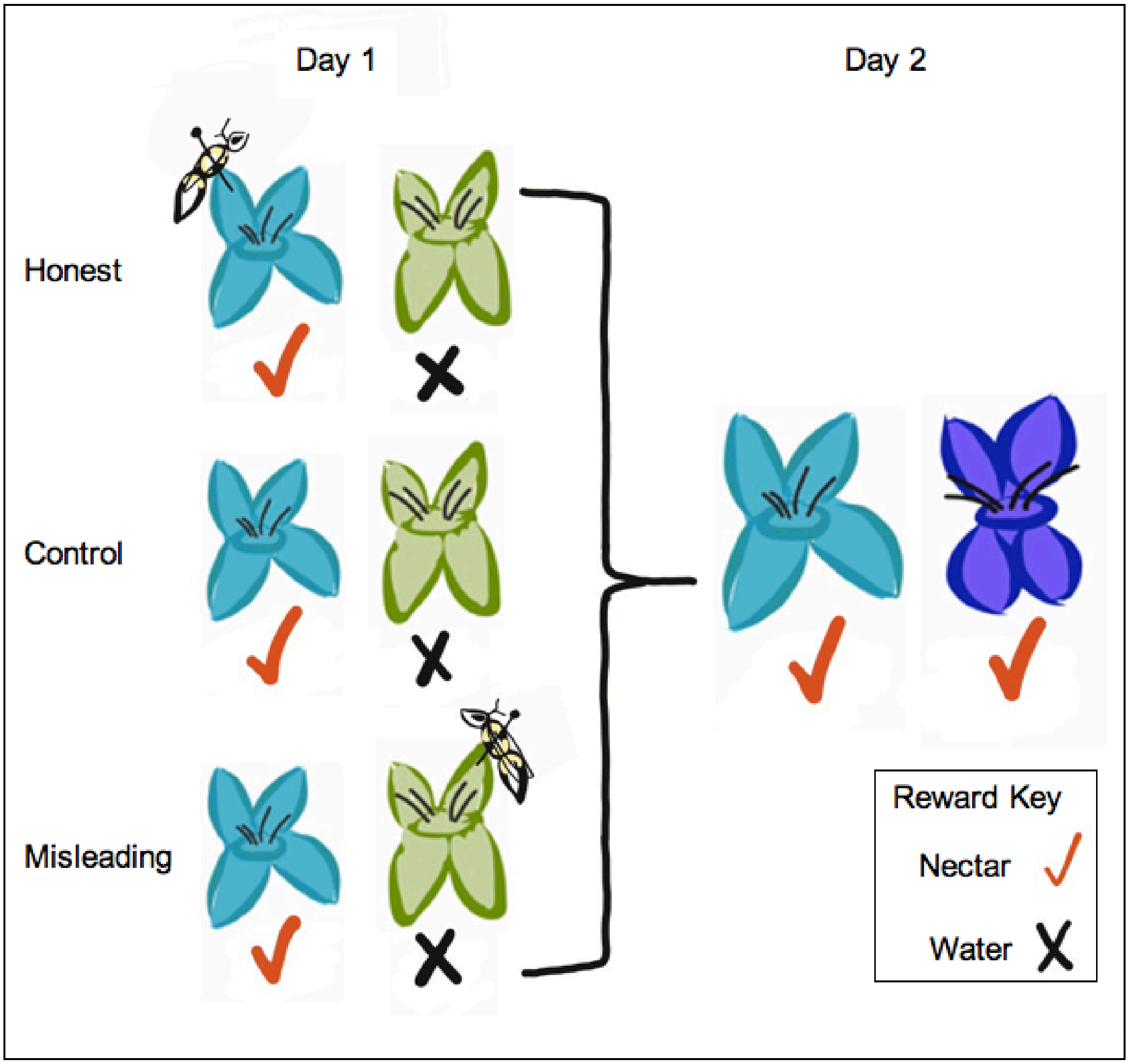

Figure 1: Diagram of experimental design for two days of bee foraging.

Flower cartoons represent the flower choices available to bees in the foraging chamber. Flowers with a check mark beneath them were filled with a rewarding 1 M nectar solution and X represents flowers filled with not rewarding water. Pinned bee represents social cue.

Data Analysis

We analyzed data in R version 3.6.3 (R Core Team 2020), including data organization with the dplyr package (Wickham et al. 2020). First, to determine whether social cue condition was correlated with preference for either flower available in a foraging bout, we compared the average proportion of visits to blue flowers on each day to random foraging (0.5 proportion of visits to blue flowers) for each social cue condition and the control group by using G-tests of goodness of fit in the R package RVAideMemoire (Hervé 2020).

To test the effect of social cues, we compared the foraging choices of bees across the three social cue groups. We used generalized linear mixed effects models (GLMMs) with binomial errors to compare the foraging behavior of bees in different social cue conditions to each other: first across days and then, in separate models, within each day. To fit the models, we used the glmer function of the lme4 package in R (Bates et al. 2020). Individual bee identity was nested within colony identity and included as a random intercept. For the model that compared conditions across both days, we included the interaction between social cue and day of foraging (i.e., training vs. test) to determine whether the effect of social cue changed over time. For the models that compared the effect of conditions within each day, the predictor variable was social cue condition and there was no interaction effect. The response variable for all models was the binomial counts of visits to blue flowers as opposed to not-blue flowers (either green or purple, depending on the day of foraging).

We also tested the effect of both social cue and day of foraging on the total number of rewarded visits that bees completed during their 30-minute foraging period. We used the lmer function of the lme4 package in R to run a linear mixed effects model. The response variable for this model was the total number of visits to flowers in which bees received a reward. The main effects in this model were social cue condition, day of foraging, and the interaction between them. We included bee identity nested in colony identity as one random intercept term.

Results

Day 1- Foraging in the Presence of Social Cues (Training)

Both social cues and floral rewards influenced foraging choices on Day 1 (Figure 2, Day 1). Bees in the control group (with no social cue) visited the rewarding, blue flower more often than would be expected by chance on Day 1 (mean ± standard error (SE) proportion of visits: 0.63 ± 0.03, $N = 42$ bees; G-test of goodness-of-fit against expected 0.5: $G = 19.02$, $p < 0.001$). Bees in the honest social cue condition also visited the rewarding flower more often than expected by random chance (mean ± SE: 0.75 ± 0.03: $N = 36$; $G = 63.60$, $p < 0.001$). Bees in both the control group and honest social cue group still visited the non-rewarding flower: 24.9% of visits for bees in the honest condition and 37.5% of visits for bees in the control condition. By contrast, for bees in the misleading condition, the proportion of visits to rewarding flowers was not significantly different from chance (mean ± SE: 0.44 ± 0.03: $N = 44$; $G = 4.47$, $p = 0.034$).

In comparing all groups of bees to one another on Day 1, we found that bees trained with misleading social cues visited the blue flower significantly *less* often than bees in the control group (GLMM $F = 1.038$, $p = 0.014$) or bees trained with honest social cues ($F = 2.13$, $p <$ 0.001). In contrast, bees trained with honest social cues visited the blue flower significantly *more* often than control bees (GLMM $F = 1.09$, $p = 0.021$).

Day 2- Foraging Without Social Cues (Testing)

On the second day of foraging, both flowers offered a reward (Figure 2, Day 2). Bees in the control and honest social cue groups no longer visited the blue flower more often than random chance (Control mean ± SE: 0.49 ± 0.03: $N = 42$; $G = 0.047$, $p = 0.83$; Honest cue condition mean ± SE: 0.45 ± 0.03: $N = 36$; $G = 2.27$, $p = 0.13$). In contrast to bees in both the control and honest cue conditions and to their own behavior on the previous day, bees in the misleading condition foraged on the previously more-rewarding blue flower more often than would be expected by random chance on Day 2 (mean ± SE: 0.59 ± 0.03: $N = 44$; $G = 8.98$, $p = 0.002$). However, there was not a significant difference between groups: the blue preference of bees in the misleading condition was not greater than that of the control bees ($F = -0.70$, $p = 0.20$) or of bees in the honest cue condition ($F = -0.93$, $p = 0.11$) on Day 2.

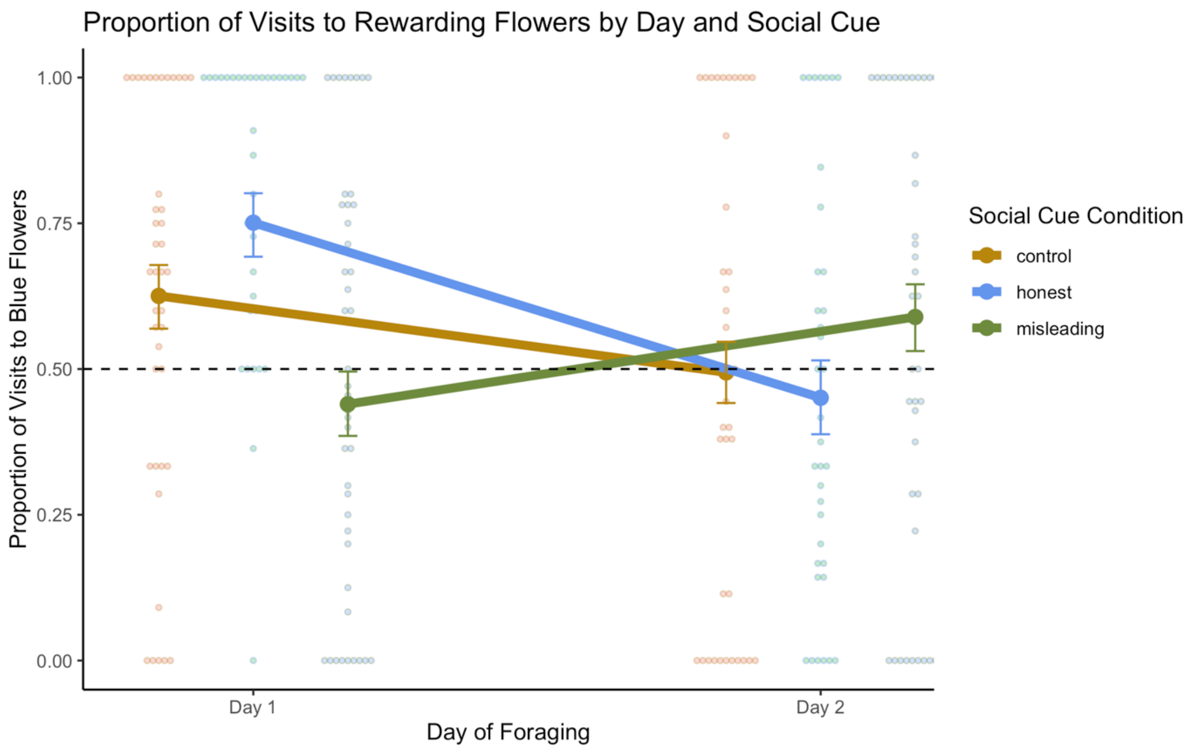

Figure 2: Bees' propensity to visit blue flowers during foraging trips over the two days.

Social cue conditions are distinguished by line and dot color. Social cues were present on Day 1 and not present on Day 2. The six large, bold dots are the mean preference for blue flowers for bees in each social cue condition on each day. Lines indicate the change in blue preference for bees in each social cue group over the two days. Each small dot in the vertical arrays represent the mean flower choice for an individual bee. Error bars are 95% confidence intervals around the mean. Dotted line set at 0.5 (random foraging).

Changes Between Day 1 and Day 2- Lingering Influence of Social Cues

Day had a significant effect on foraging in all conditions; specifically, the proportion of visits in which bees visited the blue flower differed between Day 1 and Day 2 (GLMM effect of day: chi-square = 16.98, $p < 0.001$). In addition to day, the other main effect we tested was the social cue condition, which did not have a significant effect on bees' preference for blue flowers when the two days were considered together (GLMM effect of social cue: chi-square = 3.900, $p = 0.14$). However, there was a highly significant interaction between day of foraging and social cue condition, such that bees' average preference for each day's foraging options differed between the social cue condition groups (GLMM social cue*day interaction: $F = 64.88$, $p < 0.001$).

In detail, we observed an interaction between social cue condition and day of foraging because bees in some social cue conditions decreased their preference for blue, while the other bees increased their preference for blue. The bees in the honest and control conditions decreased the proportion of visits to the blue flower on the test day (Day 1) relative to the training day (Day 2). For bees in the honest condition, the mean proportion and standard error of visits to blue flowers was 0.751 ± 0.03 on Day 1 and 0.451 ± 0.03 on Day 2. For control bees, mean proportion and standard error of visits to blue flowers was 0.625 ± 0.03 on Day 1 and 0.494 ± 0.03 on Day 2. In contrast, the bees in the misleading condition increased the proportion of visits to the blue flower from mean and standard error 0.440 ± 0.03 visits on Day 1 to 0.589 ± 0.03 visits on Day 2 (Figure 2).

Overall amount of foraging did not differ between groups. Within their 30-minute foraging periods, there were no differences between bees in the control and two social cue conditions in how many rewarded visits they made to flowers (LMM effect of social cue; chi-square = 4.19, p =0.12). In addition, there was no significant difference in this measure over the two different days (chi-square = 0.041, p = 0.84). Finally, there was no interaction between social cue condition and day for the total number of rewarded visits (chi-square = 3.27, p = 0.20).

Discussion

How do social cues influence bumble bee foraging after the cue is no longer present? We found that social cues influenced future foraging choices when the social cue was misleading. Specifically, bees in the misleading condition displayed a preference for the resource that had been more rewarding than an alternative on the previous day, but that was no longer the better choice (Figure 2). The foraging choices of bees in the honest and control groups on Day 2 aligned with our expectation for how bees would forage if, on Day 1, they did not invest time and energy into learning the characteristics (such as color) of the flower they were visiting.

Social cues are an influential shortcut for foraging

We found that bees that foraged in an environment with an honest social cue biased their foraging toward the flower with the cue. On Day 1, bees that were presented with an honest social cue foraged on the rewarding, blue flower more often than would be expected by random choice and significantly more often than did bees presented with no social cues. This result is consistent with many empirical and theoretical studies that describe the value of social cues for foragers. Theory predicts that social cues are typically consistent with the best, most recent information a forager can get (Rendell et al. 2010). This power of social cues for communicating time-sensitive information is also seen in experiments in which foraging bumble bees follow novel social cues even if the cues conflict with the foragers' own previous experiences (Leadbeater and Chittka 2009; Dunlap et al. 2016). Social cues are a foraging shortcut in that they can save substantial time relative to learning information through trial and error (Kawaguchi et al. 2006). Indeed, the burden of taking time to learn is seen in field experiments of bee foraging. For example, foragers' accuracy in identifying the most rewarding flower comes at the expense of foraging speed (Chittka et al. 2003), though we did not observe any differences in foraging speed between either of the social cue conditions or control group in our experiment. However, while honest social cues may function as a useful shortcut while present (bees followed honest social cues on Day 1), once the honest cues were absent on Day 2 of our experiment, bees did not appear to be influenced by their experience with blue flowers and their rewards (i.e., honest condition bees did not prefer blue flowers on Day 2), in contrast to the bees that were trained with misleading cues.

On Day 1, bees trained with misleading cues chose to follow that cue (and thus received no reward) on more than half of their flower visits. Following misleading social cues poses a clear risk to foraging efficiency. In nature, misleading social cues may come from other species of bees. There is ample evidence that bees follow social cues from heterospecifics (Slaa et al. 2003; Dawson and Chittka 2012; Romero-González, Solvi, Chittka 2020). However, these cues may not be valuable when the heterospecific is aggressive and poses a threat, as in stingless bees (Slaa et al. 2003), or when the heterospecific is collecting pollen and nectar that are not preferred by the forager. Bumble bees can learn to ignore heterospecific social cues when cues from that species have been misleading in the past (Romero-González et al. 2020).

Despite the risks, adherence to misleading social cues—even when the associated floral resources offer little or no reward—may still be valuable to bees. For example, in nature, flowers have ephemeral blooming peaks and their nectar and pollen deposits can spontaneously refill throughout the day (Thomson et al. 1989) or produce more nectar after being stimulated by a previous forager (Castellanos et al. 2002). Thus, a flower that contained no reward in the past may now contain one, and a social cue could indicate to foragers that this change has occurred.

Even with an honest social cue, bees still sample less-rewarding flowers

Bumble bees gather information about changes in their environment by consistently sampling the flowers that occur in their foraging range (Dunlap et al. 2017). In previous studies, researchers have found that, while sampling a flower that was previously unrewarding is most advantageous in an environment where rewards fluctuate over time, many foragers in stable environments consistently sample potential resources (Keasar et al. 2013; Evans and Raine 2014).

Bees also sample flowers that have offered no reward in the past. The bees in our study that were trained with honest social cues pointing them to the sole rewarding flower still sampled the other, non-rewarding flower on 24.9% of visits during their foraging bout on Day 1 (Figure 2). Previous researchers have described these “errors” in flower choice as potentially adaptive. For example, Evans and Raine (2014) found that bumble bees (*Bombus terrestris*) that were more “error-prone” (i.e., more likely to sample a flower that was consistently less rewarding than an alternative flower) than other foragers were also quicker to discover novel food sources.

Misleading social cues and learning

The primary finding of this study is that the reliability of social cues drove changes in foraging behavior on subsequent foraging trips. More specifically, on Day 2, bees preferred the previously rewarding flower only if they experienced misleading cues on the previous day, and not if they had foraged without cues or with honest cues. Bees trained with misleading social cues displayed this preference even though both the familiar blue and novel purple flowers were equally rewarding.

One mechanism that may explain the differences in behavior between groups on Day 2 is that the bees in the misleading social cue condition learned to associate blue flowers with reward on Day 1, and the others did not. We would expect that a group of foragers that did *not* learn to associate blue flowers with reward on Day 1 would *not* be biased by out-of-date information that blue flowers offered the best reward once it was no longer true the next day. In our study, bees trained with honest cues or no cues exhibited an essentially equal probability of foraging on either flower type on Day 2, i.e., they did not exhibit a bias toward blue flowers. In contrast, bees trained with a misleading cue did show a bias toward the blue flower on Day 2, even though it was no longer more rewarding. This difference between social cue conditions may indicate that misled bees learned on Day 1 that the blue flower was rewarding and thus preferred it to the novel flower the next day, but bees exposed to honest cues did not learn to associate reward with the blue flower on Day 1 and thus did not prefer it on Day 2.

Our findings are consistent with our hypothesis that bees trained with reliable social cues do not learn additional associations between flower color and reward. This idea in turn is consistent with social learning theory that predicts that foragers that copy others do not necessarily learn the information that drives the actions they are copying (Laland 2004). In empirical research of other animal study systems, copying and learning are similarly disconnected. For example, zebrafish that follow a conspecific leader to a shoaling location (McAroe et al. 2017), and pigeons that follow other foragers to cached food (Giraldeau and Lefebvre 1987) are unable to find that location afterwards unless they search for it themselves. The work presented here is distinct in terms of focusing on a highly simplified, non-geographic outcome (choice between two simple artificial flowers differing only in color) as opposed to a geographic or spatial outcome (shoaling or cache location). Moreover, previous work has focused on dynamic social cues from living conspecifics that can literally be followed in real time. In other words, no trial-and-error learning is required by the follower. In our work, individual bees were presented with a static social cue—a dead conspecific attached to a flower—and then later had to make foraging choices on their own. Thus, our work suggests a potentially stronger basis for the connection between social cues and learning than in previous studies, in particular that social information may affect learning even when personal trial-and-error is also involved.

Limitations and future studies

As described in the Methods section, our study was designed to avoid confounding the signal that the rewarding flower was better. Bumble bees exhibit an innate preference for blue flowers (Heinrich et al. 1977; Keasar et al. 1997; Skorupski and Chittka 2010), so our blue flower was always rewarding. This design prevented us from having to disentangle the effects of innate color preference, social cue, and reward on bees' choices. A limitation of this design, however, is that we do not know how bees would respond to a rewarding green flower and a not rewarding blue flower, though we have no reason to expect that this response would vary between social cue conditions. We also chose to set up the experiment so that, on Day 2, bees were not presented with a green flower as on Day 1, but instead a novel purple flower. We chose this option in order to disentangle a potential association between blue flowers and reward from the separate association between green flowers and a lack of reward. Our design was thus developed such that bees on Day 2 were incentivized to forage because rewards were present and so that they would have no reason to avoid the purple flower (except, perhaps, for bees' innate blue preference, though an innate preference should not vary between the groups of bees that we compared) or to prefer it over blue. Future studies could incorporate a wider variety of social and floral cues to gain deeper insight into cognition in foraging bees, such as the impact of multiple social cues or the continued influence of social cues over longer time scales.

Conclusion

Bumble bees take on the myriad challenges of foraging by following social cues and comparing those cues with information gained through their own experience of trial-and-error on previous days. Our work is consistent with the idea that bees learn more information when social cues and experience conflict, rather than align. This study adds to a growing body of literature that describes the complex ways that animals integrate information from various sources while foraging.

Chapter 2

Bumble bees do not use social cues after exposure to a neonicotinoid pesticide

Abstract

Neonicotinoid pesticides have a broad range of sublethal effects on insect behavior. For example, bees that are exposed to sublethal doses of neonicotinoids show a diminished ability to learn while foraging. However, little is known about how neonicotinoid exposure influences bees' use of social cues, which are a common shortcut to foraging efficiency, especially when a foraging task is difficult. To investigate the effect of pesticides on social cue use, we examined the foraging behavior of the bumble bee *Bombus impatiens*, comparing those who were exposed to the neonicotinoid pesticide thiamethoxam to unexposed controls, across three different social cue conditions. Social cues were either absent, honest (associated with a rewarding flower), or misleading (associated with a not rewarding flower). We hypothesized that, if neonicotinoids impair bumble bee learning, then bees may compensate for this impairment by relying more heavily on social cues from fellow bees. We found that, contrary to our hypothesis, bees that were exposed to pesticides did not align their foraging choices with the information provided by social cues. Our results may explain why groups of bees (but not individuals) are less efficient pollinators after pesticide exposure. Pesticides may impair bees' ability to access some emergent benefit of group foraging, such as the communication between individuals that facilitates reward identification.

Introduction

Neonicotinoid pesticides are the most prevalent class of insecticide used in the United States (Jeschke et al. 2011; Goulson 2013; Simon-Delso et al. 2015). These pesticides persist for multiple years in soil (Bonmatin et al. 2005) and spread far from the site of application; for example, in a nationwide survey of 48 streams, 63% of streams had detectable levels of neonicotinoids (Hladik et al. 2015). Neonicotinoids also have a broad range of detrimental effects on animal development, behavior, and survival. For example, previous studies have found that exposure to neonicotinoid pesticides is associated with damage to organ development in rats (Bal et al. 2012), diminished foraging resources for insectivorous birds (Hallmann et al. 2014), and changes in how frogs (Lee-Jenkins and Robinson 2018) and honey bees (Zhang and Nieh 2015) respond to predators. Neonicotinoid exposure at relatively minute levels can also be lethal to a range of non-target aquatic invertebrates (Morrissey et al. 2015) and bees (Rundlöf et al. 2015).

Although less immediately apparent, the sublethal effects of pesticide exposure on animal cognition may have far-reaching ecological implications. For example, bees that have been exposed to neonicotinoids as juveniles exhibit impaired learning as adults (Smith et al. 2020). When exposed bees learn to forage, they are capable of learning from fewer sensory modalities than unexposed bees (Muth et al. 2019) and their efficiency in foraging tasks does not improve with experience (Whitehorn et al. 2017). In some species, bees that are exposed to pesticides change which flowers they visit, compared with those who are not exposed (Almeida et al. 2021). Of considerable concern is the impact of exposure to pesticides on bees' ability to pollinate crops. For example, Stanely et al. (2015) found that bumble bees foraging in groups after exposure to neonicotinoid pesticides were less efficient pollinators than groups that were not exposed to pesticide. However, in the study, the difference between groups of foragers did not seem to be the sum of individual-level effects, as individual bees in their study did not exhibit impaired foraging ability after exposure to pesticides (Stanley, Garratt, et al. 2015). One potential explanation for this discrepancy between group- and individual-level foraging activity is that pesticide exposure may diminish some emergent benefit of group foraging, such as communication between individuals that facilitates efficient identification of the most rewarding resources.

While foraging, bumblebees communicate passively through the use of social cues, preferentially visiting flowers where they see the visual cue of a conspecific foraging (e.g., Leadbeater and Chittka 2007). Although passive, these social cues can strongly influence bees' choice of flowers, even if the cue is not consistently accurate (Dunlap et al. 2016). In other species, pesticide exposure can change animals' use of sensory cues. For example, zebrafish exposed to the pesticide chlorpyrifos decreased their response to olfactory social cues about the presence of a predator (Volz et al. 2020). However, little is known about how this effect of pesticide exposure on conspecific social cues applies to bees' use of visual social cues.

To address this gap, we tested the effect of thiamethoxam (a commonly used neonicotinoid pesticide) exposure on bumble bee (*Bombus impatiens*) use of both honest and misleading social cues in a laboratory foraging arena.

Methods

Study System

We used bumble bees (*Bombus impatiens)* from four colonies obtained from Koppert Biological Systems (Howell, Michigan). We fed the bees an *ad libitum* supply of pollen (Koppert Biological Systems, Howell, MI) and a 1 M sugar water solution. Each colony was placed in a plastic container (0.600 x 0.416 x 0.165 m) with large ventilation panels covered in metal screen. Before experiments, a selection of workers was placed in smaller subcolonies that were located inside of the main colony box, so that we could easily manipulate and/remove these bees while maintaining their exposure to natural queen pheromones. The subcolony boxes measured 22.2 x 16.8 x 14.0 cm and were also made of plastic containers with sides covered in metal screen.
The bees used in this experiment were also used in the experiment that is described in Chapter 2. Some of the data included in this report are also included in that publication, though the analysis and interpretation in that chapter focused on the effects of social cues (and that chapter does not include any data on pesticide exposed bees), while this report focuses on the effects of pesticide exposure.

Pesticide Exposure

Three days before trials began, bees were assigned to pesticide-exposed and unexposed treatments by subcolony. Unexposed bees were fed *ad libitum* pollen and sugar water solution as they had been. Pesticide-exposed bees were fed the same pollen, but their sugar water solution included 10 parts per billion thiamethoxam for the duration of the week. This solution was prepared by serial dilution of 10 mg dry thiamethoxam (Cayman Chemical Company, Ann Arbor, MI) dissolved into 1 L hot water. 0.5 mL of this solution was then added to 499.5 mL of our usual sugar water solution. We chose 10ppb as a field-realistic concentration of thiamethoxam as in many other studies (e.g., Stanley and Raine 2016; Shi et al. 2017; Ma et al. 2019; Arathi H S and Bernklau 2021), given that previous studies have found concentrations of thiamethoxam ranging from 1-50 ppb in the nectar and pollen of crop plants and 1-9 ppb in the nectar and pollen of non-crop plants growing at the margins of agricultural fields (Goulson 2013).

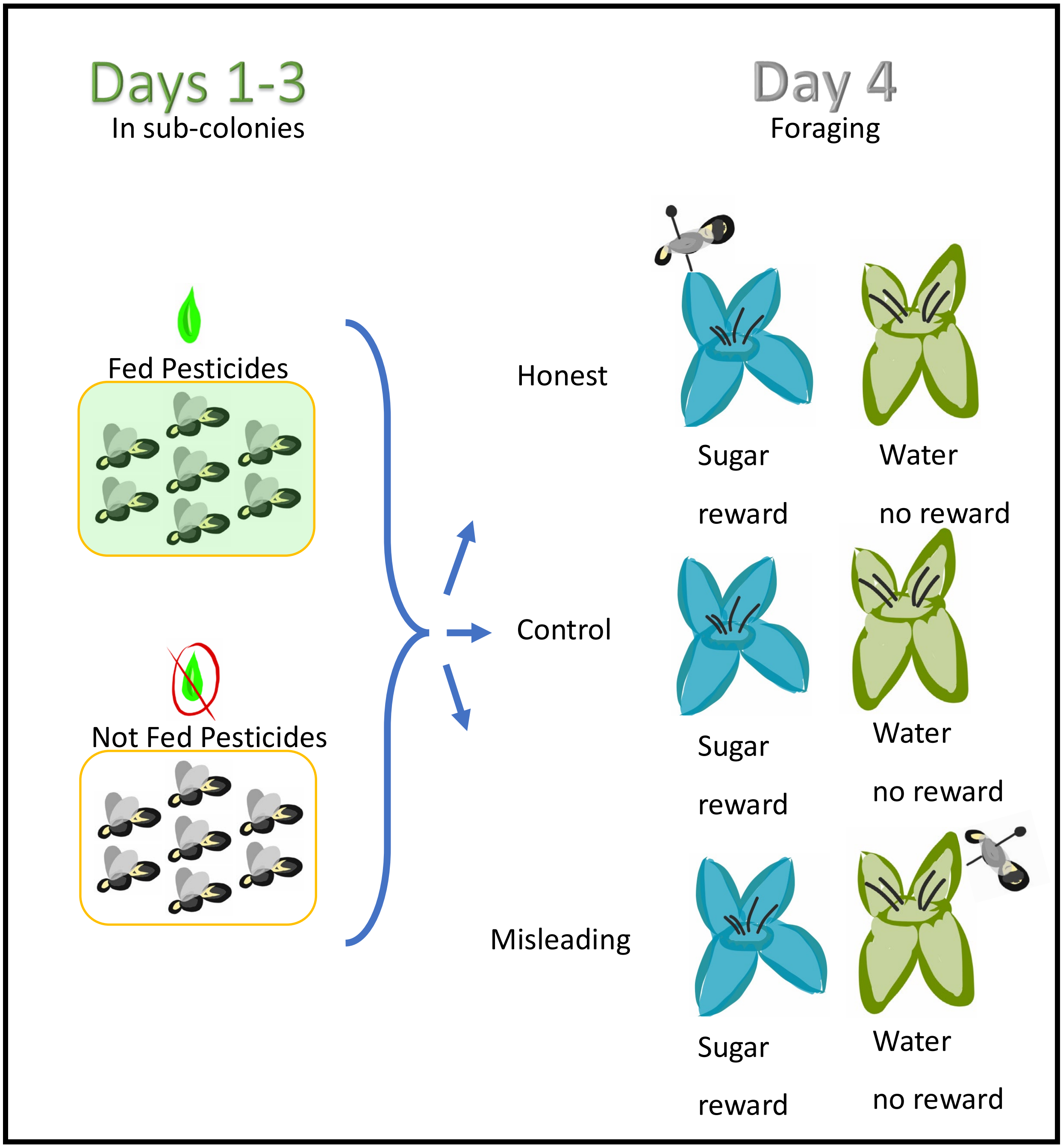

Figure 1: Diagram of experimental design for neonicotinoid exposure and foraging trials.

Flower illustrations represent the flower choices available to bees in the foraging arena. Flowers with a check mark beneath them were filled with a rewarding 1 M sugar water solution and those with an X were filled with water (not rewarding). Pinned bee represents social cue.

Foraging Arena

The artificial foraging arena was a large (0.75 x 2.27 x 0.74m) space with white plastic sides, a wire screen top, and a green plastic base that had 14 artificial flowers set into it. We divided the total space of the foraging arena into seven sub-enclosures, so that we could test up to seven bees simultaneously and separately, as only one bee was placed into each sub enclosure at a time. The sub-enclosures (42.55 x 30.18 x 17.78 cm) were made of plastic painted white (so bees could not see each other) with a metal screen top that was open to air and light. The foraging arena was maintained at 28˚C by incandescent light bulbs that illuminated the sub-enclosures. Bees did not live in the sub-enclosure nor in the larger foraging arena. They were placed into the sub-enclosures only during trials. Before and after trials, the bees continued to live in the sub-colony with exposure to the main colony.

Each sub-enclosure contained two artificial flowers. Each flower was equipped with a Microsensys Radio Frequency Identification (RFID) reader. This reader could be triggered to dispense a droplet of water or sugar water solution by a bee wearing an RFID tag. We attached mic3-TAG RFID tags (1.9 x 1.6 x 0.5 mm; Microsensys, Gainesville, FL) to each bee's thorax one week before trial. In this way, the foraging arena was designed to track the flowers each bee visited. The RFID readers could read tags that were within a 3-4 mm distance. The readers did not dispense a droplet of liquid if the reader was triggered by the same bee's tag with a 30 second period, so that bees could not sit in the center of a flower and continuously receive sugar-water rewards but instead had to leave the flower and return again to get a new reward.

The flowers in the foraging arena were 3-D printed and painted with acrylic paint (Crayola, Forks Township, Pennsylvania). Blue flowers consistently dispensed sugar water, green flowers dispensed only water, which is not a reward. In our experiment, we chose to test bees' ability to learn flower colors because previous studies have shown that bees readily make these associations (e.g., (Gumbert 2000; Kunze and Gumbert 2001; Worden and Papaj 2005; Kaczorowski et al. 2012). In all trials, the colors of the rewarding and non-rewarding flower were consistent in order to align the sensory cues that indicated which flower was the better choice. In this way, we measured bees' overall response to the social cue and did not have to disentangle the rate at which bees learned to identify the rewarding sugar water and their inherent preference for blue flowers (Raine et al. 2006). Also consistent was that bees were all naive to the foraging arena before the foraging test and rewards were consistent in quantity and type. We kept these cues rigorously consistent as recommended by other researchers in the area of animal cognition (e.g., Rowe and Healy 2014).

We cleaned the foraging arena, sub-enclosures, and flowers with a 70% ethanol solution between all trials to remove any potential pathogens or scent marks.

Social Cues

We compared the foraging behavior of bees trained with honest, misleading, or absent social cues. The social cue was a dead, frozen conspecific, a decoy that is commonly used in research on foraging in bees (e.g., Worden and Papaj 2005; Kawaguchi et al. 2006). Frozen bees were pinned to either the rewarding, blue flower (in the honest condition) or the non-rewarding green flower (in the misleading condition). For the control group of bees, flowers had no social cues (Figure 1).

Foraging Test

Before the foraging test, individual bees were removed from both the pesticide-exposed and unexposed subcolonies and placed individually in 50ml falcon tubes in a dark cabinet while they were deprived of food for at least two hours in order to enhance foraging as in previous studies (e.g., Rademaker et al. 1997; Manson et al. 2010).

For the foraging test, we placed each bee by itself into a sub-enclosure in the foraging arena (up to seven bees foraged simultaneously but were separated into different sub-enclosure and could not see each other.) We recorded the number of times each bee visited each flower type (blue or green) in a 30-minute period.

After the foraging test, bees were removed from the foraging arena and placed back into the subcolony they were removed from. They were then fed *ad libitum* pollen and sugar water.

Data Analysis

We conducted all analyses in R version 3.6.3 (RStudio Team 2020). Our analysis consisted of a series of generalized linear mixed models (GLMMs) using the lme4 package (Bates et al. 2020). For these models, we tested the statistical significance of main effects and interactions using the ANOVA function of the car package (Fox et al. 2021)

First, we tested the impact of social cue condition and neonicotinoid exposure as main effects on total number of visits bees in each group collectively made to flowers in the 30-minute foraging period. For this analysis, we used a GLMM with poisson errors in the lme4 package. Bee identity, nested within colony identity, was included as a random effect.

Next, to test the impact of social cue on bee foraging, we ran three GLMMs with binomial errors. The first GLMM tested social cue condition, neonicotinoid exposure, and the interaction between those two as main effects. We performed two more GLMMs on subsets of the data to better understand the direction of the interaction between social cue and neonicotinoid exposure. The second GLMM tested only bees that were exposed to neonicotinoids, with social cue condition as the sole main effect. The third GLMM tested only bees that were not exposed to neonicotinoids, again evaluating the main effect of social cue condition. All GLMMs tested the impact of the main and random effects on blue preference, the binomial count of visits that bees in each group made to the rewarding, blue flower or the not-rewarding green flower.

We used mixed-effects models because our experiment included repeated measurements of the same individual bees (i.e., if one bee made ten flower visits, that is represented in our data as ten data points), and multiple bees came from the same colony. Therefore, our models included both individual bee identity and colony identity as random effects. Bee identity was nested within colony identity.

Results

Bees in all groups foraged successfully in the artificial foraging arena. In each 30-minute time period, bees made between 1 and 17 choices of one flower or the other (Table 1). Bees that did not forage were excluded from analysis. Our GLMM showed that neither neonicotinoid exposure nor social cue condition had a significant effect on the number of visit that bees made to flowers during their 30-minute foraging period (Effect of social cue: chi-square=0.16, p=0.92; Effect of Neonicotinoids: chi-square=0.61, p=0.43; Social cue*neonicotinoid interaction: chi-square=0.38, p=0.83.)

Table 1: Number of bees and amount of foraging.

Number of bees used in each social cue condition, range of droplets (of water or sugar water) collected by bees in each group, and mean number of droplets per bee collected from the foraging arena.

Neonicotinoid	**Social Cue**	**Range of Visits**	**Mean Visits**	**Number of Bees per Colony**				
				1	2	3	4	Total

Unexposed	No Cue	2-15	7.1	14	18	22	30	84
	Honest	1-15	6.7	8	14	18	32	72
	Misleading	1-17	7.0	12	20	28	28	88
Exposed	No Cue	1-10	6.1	6	19	20	0	45
	Honest	1-15	6.3	18	10	24	0	52
	Misleading	1-14	6.5	12	8	14	0	34

Effect of Social Cues and Neonicotinoids on Preference for Rewarding Flowers

Overall, our analysis showed an interaction between social cues and neonicotinoids in their combined effect on bee foraging. Specifically, our GLMM of all foragers showed a significant interaction between neonicotinoid exposure and social cue condition on bee preference for blue flowers neonicotinoid*social cue interaction: chi-square=17.16, p<0.001). The other main effects of this model were neonicotinoid exposure alone, which was not significant (effect of neonicotinoids; chi-square=0.063, p=0.80), and social cue treatment, which was significant (effect of social cues: chi-square=37.97, p<0.001). The significant effect of social cue treatment is likely driven by unexposed bees, and those data are interpreted in the previous chapter and will not be discussed at length in this chapter.

We used subsequent GLMMs to analyze the direction of the interaction between social cues and neonicotinoid exposure. In our GLMM of only neonicotinoid-exposed bees, we found that these bees, regardless of social cue condition, chose blue flowers at about the same rate; there was not a statistically significant difference in proportion of visits to blue flowers between the three social cue groups (effect of social cue: chi-square=1.68, p=0.43). For these neonicotinoid-exposed bees, the mean ± standard error (SE) proportion of visits to blue flowers for bees in the honest social cue condition was 0.59 ± 0.04; for bees in the misleading social cue condition, it was 0.57 ± 0.05; and for bees in the no social cue condition, it was 0.65 ± 0.04.

In contrast to the neonicotinoid-exposed bees, the unexposed bees appeared to use social cues if they were present, such that these bees exhibited a significant difference in their level of preference for blue flowers depending on which social cue condition they had foraged in (effect of social cue: chi-square=52.70, p<0.001). Unexposed bees that foraged with honest social cues exhibited the strongest blue preference of all groups (mean ± SE: 0.75 ± 0.03; N=72) and unexposed bees that foraged with misleading social cues exhibited the weakest blue preference of all groups (mean ± SE: 0.44 ± 0.03; N=88). In between these two were unexposed bees that foraged without social cues, which exhibited a preference for blue flowers (mean ± SE: 0.63 ± 0.03) that was similar to the three groups of pesticide-exposed bees.

The results of these last two models are consistent with an absence of social cue use among neonicotinoid-exposed bees, in contrast to unexposed bees which do make flower choices that align with social cues (Figure 2).

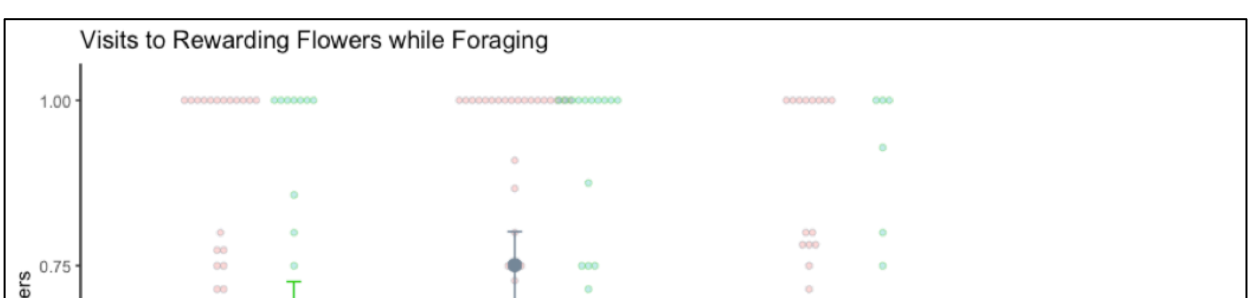

Figure 2: The extent to which bees chose the blue flower while foraging.

Pesticide exposure is indicated by point color. Error bars show 95% confidence intervals around the mean. Large, bold dots are the mean preference for blue flowers for bees in each social cue and pesticide exposure group. Small green and pink dots in vertical arrays represent the mean flower choice for each individual bee. Error bars are 95% confidence intervals around the mean. Dotted line set at 0.5 (random foraging).

Discussion

In this study, we evaluated the role of neonicotinoid pesticides in bumble bees' use of social cues while foraging. We expected that bees might increase their reliance on social cues if their cognition was damaged after exposure to pesticides. Specifically, we expected that pesticide-exposed bees would choose to visit a flower with a social cue on it more than their unexposed peers did. To our surprise, we found that pesticide-exposed bees did not align their foraging with social cues. This result contrasted starkly with that in unexposed bees, which tended to follow social cues even if they were misleading.

Pesticide-exposed bees did not use social cues

Bees exposed to a neonicotinoid pesticide did not bias their foraging toward a flower with a social cue on it, as their unexposed peers did. More specifically, among unexposed bees, those who foraged without a social cue chose blue flowers on 63% of their visits; bees exposed to honest social cues (on blue flowers) chose blue flowers significantly more often, and those exposed to misleading social cues (on green flowers) chose blue flowers significantly less often. This pattern did not hold for pesticide-exposed bees. Like unexposed individuals, pesticide-exposed bees showed a preference for rewarding flowers, but unlike unexposed bees, this preference was neither increased by honest social cues nor decreased by misleading cues.

Our initial hypothesis that pesticide exposure would increase bees' use of social cues was rooted in the logic that completing a difficult task (foraging while cognitively impaired) should be easier with external support (social cues), a logic supported by other experiments on cognition in bees (e.g., Baracchi et al. 2018). In contrast, our results suggest that one aspect of the cognitive impairment itself is the loss of social cue use as an external learning support.

Our results fit into the broader body of research, which shows that pesticide exposure hinders the myriad strategies bees use to forage efficiently. For example, Siviter et al (2021) found that bumble bees exposed to imidacloprid, a different neonicotinoid pesticide, wasted energy while foraging because they did not visit the flowers that were closest to them and instead flew to flowers that were farther away. These results are similar to ours; in both studies, bees did not use visual cues (flower proximity and social cues) as shortcuts in the same way as unexposed bees. To speculate on a broad mechanism, pesticide exposure appears to negatively impact bees' ability to make comparisons between flowers, as if the bees cannot synthesize multiple pieces of information (e.g., both flower identification and flower proximity) as unexposed bees do.

Another connection between our study and the one by Siviter et al (2021) was that the two different detrimental effects of neonicotinoids we observed may interact. Siviter et al. found that pesticide-exposed bees made suboptimal choices. Considering this result alone, one might hypothesize that this inefficiency is ameliorated when bees have access to the social cues of more efficient, unexposed foragers. Yet, our results indicate that this explanation is unlikely. Neonicotinoids may thus have compounding effects on insect cognition, i.e., negative direct impacts on learning may be heightened by reduced ability to utilize social cues. Future studies should investigate both the mechanisms by which neonicotinoid pesticides affect foraging and the interaction between the effects of neonicotinoids on the information bees learn themselves through trial-and-error and the information bees learn from others through social cues.

Decreased use of social cues may explain group-level reduction in pollination efficiency

The impact of pesticide exposure on bees' use of social cues may have broader implications for ecosystem services such as pollination. Previous research shows that neonicotinoid exposure can impair pollination (Goulson 2013; van der Sluijs et al. 2013). For example, Stanley et al (2015) found that neonicotinoid exposure decreased the overall pollination efficiency of a group of bumble bee foragers, relative to that of an unexposed group. Interestingly, they did not see this effect at the individual level; individual bees pollinated just as well whether they were exposed to pesticides or not. This difference between individuals and groups in their response to pesticide exposure may imply that there is some emergent benefit of foraging in a group, and that benefit is lost after pesticide exposure. One obvious emergent benefit of group foraging is that foragers in a group can learn from one another's social cues. We see this benefit of social cues in our study. Among unexposed bees, foragers with access to honest social cues visited rewarding flowers at significantly higher rates (and thus collected sugar water more efficiently) than bees with no social cues. Previous researchers have also found this correlation between social cue use and foraging efficiency in, for example, alignment with pheromone-marked trails by ants (Czaczkes et al. 2011), orientation by colony mates' flight directions in Cape gannets (Thiebault et al. 2014), and observation of the movement of shoal members in guppies (Day et al. 2001). Future studies should investigate the role of pollinator social cues on plant fitness outcomes.

Conclusion

Neonicotinoids are the most heavily used class of insecticides; they spread into soil and water and they accumulate in the bodies of animals (Goulson 2013), some of which are essential to human well-being. Neonicotinoid exposure leads to a variety of sublethal effects in beneficial insects, changing the subtle but imperative interactions between these insects and their environment. We studied the influence of a neonicotinoid pesticide on bees' social cue use while foraging. Social cues are a key component of how bees and other animals efficiently forage in the complex, constantly changing landscape of floral rewards. One possible implication of our study is that decreased use of social cues may explain why neonicotinoid pesticides reduce pollination efficiency among groups of foragers, even though an individual forager in isolation appears to be unaffected by neonicotinoid exposure (Stanley, Garratt, et al. 2015). It is critical that future researchers investigate how exposure to agrochemicals impacts not only individuals, but the communication between individuals that facilitates pollination and other ecological functions that arise from group efforts.

Chapter 3

Integration across dimensions of the 4DEE framework: Seven strategies from existing ecology assessments

Abstract

The 4-Dimensional Ecology Education (4DEE) framework is a guide for undergraduate ecology teaching. Framework creators encourage instructors to teach lessons, units, courses, and curricula that integrate across the four dimensions of the framework, which are Ecology Concepts, Ecology Practices, Human-Environment Interactions, and Cross-cutting Themes. 4DEE elements range from life history to informatics to ethics, touching on a range of disciplines. The disciplinary breadth contained within 4DEE may present a challenge for instructors planning to integrate across dimensions. Despite the challenges, integrating diverse disciplinary content with ecology concepts may help students contextualize coursework and, in their future careers, collaborate on solutions for ecological problems. However, there is little research on how ecology instructors *already* integrate information from various disciplines represented in the 4DEE dimensions. To address this gap, we used qualitative content analysis of ecology assessments to evaluate how instructors measure student ability to integrate across the 4DEE dimensions. To guide this analysis, we drew on Svetlana Nikitina's categories of interdisciplinary teaching. Seven themes of integration across 4DEE dimensions emerged from

our analysis of course documents: *Addressing Problems in the Environment*, *Addressing Problems of Racism*, *Contextualizing in the Humanities*, *Justifying Ecology in Society*, *Connecting Ecology and Evolution*, *Tailoring Practices to Research Questions*, and *Emergent Patterns in the Natural Sciences*. We discuss the strengths and limitations of each of these themes for teaching ecology and recommend strategies for using these themes to integrate across dimensions of the 4DEE framework. Future studies can build on this research by investigating the impact of lesson and assessments that use these themes on student learning outcomes and interest in ecology.

Introduction

Integration as an Umbrella for Interdisciplinarity and its Look-Alikes

Many institutions of higher education proffer interdisciplinarity as a fundamental characteristic of their research and teaching (Graff 2016). The merits of this approach are many; interdisciplinary scholars propose that their work incorporate ideas, tools, and approaches from multiple, conventionally siloed disciplines, and in doing so produce new forms of knowledge (Moran 2010). This knowledge yields deeper understanding of one's original discipline, preparation of students for careers in which they work with multi-professional teams, and the promise of solving urgent world problems (Woods 2007).

Indeed, the benefits of interdisciplinary education have political ramifications. Interdisciplinarity may disrupt the political structure of universities, where conventional disciplinary boundaries make strong distinctions between academic thought, particularly that in the natural sciences, from human concerns (Moran 2010). In addition, interdisciplinarity is lauded as a tool for shaping national change. For example, researchers have called on interdisciplinarity as a method for promoting ethical values among a rising cohort of biotechnologists in Malaysia (Hiong and Osman 2013), and for engaging critical understanding of scientific advances among citizens in the European Union (Osborne and Dillon 2008) by teaching sciences and mathematics in the context of their social, cultural, and ethical dimensions (Maass, Doorman, et al. 2019).

The powerful potential of interdisciplinary teaching is particularly relevant in ecology, a discipline in which researchers use tools from across the natural sciences to describe pressing world issues like climate change, species loss, and various forms of environmental degradation. However, ecology teaching does not always reflect the immediate relevance of these issues. For example, environmental science textbooks frequently discuss ecology topics as independent from content about everyday life, human action, or environmental impact, implying that people, both in their material needs and the consequences of their actions, are separate from their environments (Wyner and DeSalle 2020). This separation is not particularly surprising to those who have described the philosophical and cultural limitations of Western science. In particular, the limits of Western science are not inherent to science in general; for example, Indigenous sciences emphasize that humans are connected to the natural world, that all life forms are agentic, and that understanding responsibility and impact are key for knowledge production (Bang et al. 2018). Interdisciplinary teaching can be a powerful tool in guiding students through an examination of both the roots and implications of ecological scholarship. For example, evaluating ecology through a decolonial framework that emphasizes history and ethics can help generate ecological scholarship that is “more inclusive, creative and ethical at a moment when the perils of entrenched thinking have never been clearer” (Trisos et al. 2021).

Despite the benefits of interdisciplinarity in theory, interdisciplinary teaching is challenging in practice. Many of the universities that market their interdisciplinary approach rarely define what they mean by the term, let alone support interdisciplinary scholars with tangible resources (Graff 2016). At the classroom level, some instructors do identify interdisciplinary perspectives that aid in student learning of content knowledge (Bopegedera 2005). However, students may also object to extra-disciplinary lessons that appears to be “off-topic” from the central concerns of their coursework (Richter and Paretti 2009). In addition, instructors may not be willing to take the risk of interdisciplinarity. For example, instructors trained to teach The Curriculum for Agricultural Science Education, another educational framework whose creators recommended interdisciplinary teaching, did not differ from their untrained peers in their intentions to integrate science concepts into their lessons (Pauley et al. 2019). This conflicting evidence highlights important questions about interdisciplinary teaching: Do students and instructors understand the boundaries of their disciplines? Do they recognize when and how they are referencing other disciplines? Do they see value in it?

Addressing these questions and investigating the spaces between disciplines can quickly become unwieldly without a situating framework. In ecology, one such framework is 4-Dimensional Ecology Education (4DEE), which was established in 2018 and sanctioned by the Ecological Society of America (ESA) as a guide with key topics and approaches for undergraduate ecology teaching (Berkowitz et al. 2018). 4DEE is intended to be relevant even beyond undergraduate courses; the authors of the original report presented the framework and noted that, “For society in general, the 4DEE model communicates to the general public what ecology is, its interdisciplinary nature, and its use in policy and management” (Berkowitz et al. 2018).

The 4-Dimensional Ecology Education Framework

The 4DEE framework was developed by members of the ESA Committee on Diversity and Education and revised with feedback from the broader ESA community over several years (Berkowitz et al. 2018). The 4DEE framework's four dimensions are Ecology Concepts, Ecology Practices, Human-Environment Interactions, and Cross-cutting Themes. The inclusion of these four dimensions not only stresses teaching of content knowledge and research skills, but also the relevance of these topics to students' understanding that humans depend on the environment and their ability to communicate what they learn in order to address global environmental problems (Prevost et al. 2019). Indeed, the authors intend that 4DEE will empower students to take what they learn from ecology into careers outside of academia (Prevost et al. 2019).

4DEE's emphasis on career-building skills and pressing environmental problems may be an asset to students looking to find meaning in their undergraduate courses and to ecology programs that seek to support these students. In particular, Black, Latino, American Indian, and first-generation students are more likely to identify as scientists if they believe that science is helpful to their communities and families, an identity that can help students persist in science programs (Jackson et al. 2016). Students who learn ecology by practicing transferrable research skills (as in the Ecology Practices dimension) and by examining human-environment interactions (its own dimension) may find that their coursework is better aligned with their goals and values than it would be in a one-dimensional course.

Marginalized students may also thrive in the active learning pedagogy that 4DEE was designed to facilitate. Specifically, early explanations of 4DEE lessons included active learning strategies like course-based undergraduate research and case studies, an intentional illustration of how students can use skills in the Ecology Practices dimension to learn information in the Ecology Concepts dimension (Prevost et al. 2019). Previous research shows that marginalized students have particular strengths in learning through these techniques, as seen for Black men in lab-based education (Gasman et al. 2017), and for African American, Latino, Pacific Islander, and Native American students in active learning (Ballen et al. 2017) and team learning (Snyder et al. 2016) courses.

Students may also benefit from the 4DEE Framework as a starting point for interdisciplinarity. The authors of 4DEE explained that the four dimensions should be integrated together at the unit, course, and curriculum levels (Berkowitz et al. 2018). Of course, integration across disciplines is not quite the same as interdisciplinarity. First, the 4DEE dimensions do not directly map onto different disciplines. Instead, the dimensions each contain elements that tend to be primarily taught in various disciplines; for example, the disciplines of statistics and environmental sciences appear in Ecology Practices; sociology, public health, and economics appear in Human-Environment Interactions; and evolution and mathematics in Cross-Cutting Themes. Second, it is challenging to establish what "integration" means in practice, though this is not for lack of use of the term among academics. As Graff hyperbolizes:

> The discourse of interdisciplinarity is founded on the repetition, and occasional abuse, of a relatively small number of words. Beyond boundaries and borders lie borrowing, breaking, bridging, crossing, disciplinarity, hybridity, integrative, integration, interdisciplinarity, interdisciplinary, ecology of knowledge, multidisciplinary, problem solving, specialization, supradisciplinary, synthetic, transdisciplinary, unity, and unification. This is an active but often abstract discourse. This series of words is not a particularly inviting vocabulary, or often a clarifying one. The key terms seem only to

> cohere around moves away from the disciplinary. Repetition, among other elements of the discourse of interdisciplinarity, lends a quality akin to chanting an oath or a prayer of interdisciplinarity and a badge of membership. "Crossing, crossing, crossing… integrating, integrating, integrating… converging, converging, converging." (Graff 2016)

For the purposes of this study, we define integration as the combination of multiple disciplines to some degree, an umbrella term for cross-, multi-, inter-, and transdisciplinarity. Under this definition, the authors of the 4DEE Framework seem to encourage an approach to teaching ecology in which students borrow elements from a range of disciplines and combine those disciplinary ideas in some way that deepens their grasp of ecology.

Two 4DEE lesson examples described integration in one class as a process of iterative conceptual modeling with information from all four dimensions and, in another class, through consecutive activities that partnered two of the four dimensions in various combinations (Prevost et al. 2019). Beyond these published examples, little detail has been provided for how and why instructors should approach this integration. Detail would be valuable, because integration of various disciplinary elements is not generally automatic or intuitive—students can struggle to transfer even basic skills like reading, writing, and math to disciplinary coursework, especially if they are expected to learn disciplinary information in this transfer (Perin 2011). These challenges in integration are most readily apparent in assessment, since assessment is "an evidence-based argument that [multi]dimensional learning has occurred" (Laverty et al. 2016).

Rationale for This Study

In this study, we examine the extent to which instructors who teach ecology currently assess their students' ability to integrate elements from different dimensions of the 4DEE framework. By establishing this baseline, future researchers can evaluate how instructors can improve integration across 4DEE dimensions. In other words, before researchers and instructors can *improve* integration and gain the benefits of interdisciplinarity, we must have a more specific understanding of what integration means in the context of assessment and how it is accomplished by instructors who are not necessarily familiar with the 4DEE framework at all. Our guiding questions are: To what extent is integration already happening? And how does existing integration align with interdisciplinary theory?

To address these questions, we surveyed instructors who teach ecology in their courses (hereafter called "ecology-content courses"). Our survey collected information about the characteristics of each course as well as syllabi and blank assessments. We used qualitative content analysis of these course materials to locate 4DEE elements, identify their level of integration, and describe how integration occurred. We summarize these findings here and, using interdisciplinary theory, describe strategies for furthering integration to accomplish various learning goals.

Methods

Survey Distribution

We used Qualtrics XM software (Qualtrics, Provo, UT) to distribute a survey to instructors of ecology-content courses (survey included in Appendix A). Participants were asked to fill out a short survey on a course they have taught and then upload the assessments and syllabus they have used for that course. This call for summative and formative assessments included any of the following: exams, essay prompts, project instructions, activity descriptions, answer keys, or rubrics. The survey did *not* ask for examples of student work. We solicited survey respondents from January 19^{th} to April 27^{th}, 2021, through Twitter and ecology listservs such as Ecolog-L (Ecological Society of America), EcoEdList (Ecological Society of America), and those for SABER (Society for the Advancement of Biology Education Research), and ABLE (The Association for Biology Laboratory Education). We received 83 responses, of which 26 included course documents (a syllabus or blank assessments) and fit our inclusion criterion. The inclusion criterion was that survey participants must be current or recent (since 2000) instructors of college and university ecology-content courses taught in the English language. Due to our recruitment methods, our sample of survey respondents is likely to be biased toward those who were more familiar with the 4DEE framework, as the framework was advertised and discussed on several of the same listservs on which we posted the survey. Similarly, our request for course documents may have biased our sample toward instructors who already had course documents organized together, which may have been more common in instructors who had taught the course multiple times in the past, rather than newer instructors.

The study was distributed after IRB approval by the Emory Institutional Review Board (study identification number 00001509). Written informed consent was obtained from study participants on Qualtrics before they began the survey.

Content Analysis

We used directed content analysis in MaxQDA 2020 (VERBI, Berlin, Germany) to identify elements of the 4DEE framework and their level and form of integration. In directed content analysis, a coder starts with existing research to establish *a priori* codes that are likely to be of interest (such as the elements of the 4DEE framework), then, in analysis, either specifies these *a priori* codes in the context of the text or establishes new codes that represent data in the text that does not fit into one of the *a priori* categories (Hsieh and Shannon 2005).

Contextual Units

Within each assessment, codes were assigned to contextual units that each represented a single independent task. The length of these contextual units varied greatly. For exams, most questions were interpreted as independent contextual units, with the exception of groups of questions for which the answers were interrelated (e.g., a single, numbered question with multiple, lettered parts). Some large assignments, such as essays, presentations, and lab reports, were interpreted as a single contextual unit. This process for establishing contextual units was based on our perception of how many parts of an assignment a student would likely need to consider in tandem in order to accomplish an assessment task. For example, in most exams, a student does not need to consider the content of question one in order to answer question four. In contrast, in a lab report, a student will likely need to consider the introductory content of the lab in order to justify their experimental methods, for instance. We used this approach to establish contextual units because our study was primarily concerned with the integration of ideas, and we assume that a prerequisite for integration is at least keeping in mind separate ideas at the same time. A drawback of our approach is that it is difficult to use our contextual units to reliably quantify how frequently our codes occurred in our study documents. Specifically, we are limited in our ability to meaningfully compare how well-represented each element of the 4DEE framework is in the assessments we collected. For example, an element could be coded ten times in an exam and only once in a lab report, though it seems entirely possible that the student had to spend more time thinking about the element in the lab report than the exam. For simplicity of language in this paper, we refer to contextual units as questions throughout, with the understanding that these "questions" may more specifically include sets of questions, essay prompts, lab reports, and other such contextual units. A small number of contextual units were not focused on ecology content and thus were not coded for elements in any of the 4DEE dimensions; these contextual units were excluded from our study.

Identification of 4DEE Elements

Different codes were identified in the texts in each of three cycles of coding. In the first cycle, we coded the texts for the presence of any elements of the 4DEE framework. These were *a priori* codes (Mihas and Odum Institute 2019) taken from the initial report on the 4DEE framework (Berkowitz et al. 2018) and listed in Appendix D. Some codes were specified with definitions from an ecology textbook (Cain et al. 2008) or, for elements in the Cross-cutting Themes dimension, through consultation of previous publications that have discussed similar themes in other curricula (Brewer and Smith 2011; Brownell et al. 2014; Laverty et al. 2016). We added only one code during this cycle that did not originate in the 4DEE framework, and that was a general code for course-wide ecology content. This practice was useful because several assessments asked students to pose a question about or discuss any of the ecology topics they had covered in the course so far. In general, throughout the dimensions, parent codes (such as community in Ecology Concepts, fieldwork in Ecology Practices, and ethics in Human-Environment Interactions) were used as codes when a contextual unit contained content that appeared to fall into the general classification of the parent code but was not described more specifically by a sub-element. The exception to this pattern is the Cross-cutting Themes element spatial and temporal, which is a parent code that we never used in our analysis. For the spatial and temporal parent code, identifying appropriate use of this code was challenging because of the ubiquity of both space and time as concepts that govern perhaps every aspect of the physical world—while nearly every contextual unit could be said to relate to either space or time in some way, we decided to focus on the more specific aspects of space and time that were encompassed by the spatial and temporal sub-elements.

A single contextual unit could be coded for multiple 4DEE elements, and most were. Contextual units were coded with a 4DEE element if the element appeared or was strongly implied by either the question or its answer, even if we identified that the answer was wrong (in the case of selected response questions like multiple choice). As with establishing our contextual units, this inclusion of wrong answers was an intentional choice to approximate students' multidimensional thinking: a student had to think about any element that is mentioned, even if only to dismiss it as incorrect. By this same logic, elements were included even if they were not relevant for answering the question (e.g., a question about growth curves that happened to mention an agricultural context would be coded with "agricultural ecosystems").

This inclusive strategy for assigning framework codes differed from that of previous researchers who have sought to identify multidimensionality in science assessments. Specifically, the 3-Dimensional Learning Assessment Protocol (3D-LAP) used a more rigorous set of criteria to establish the presence of curriculum elements in assessments, for some dimensions establishing a list of criteria that must all be met within an assessment question (Laverty et al. 2016). This difference in coding criteria reflected our differing goals: the 3D-LAP was constructed to set a standard for faculty so that their assessments elicit elements of a particular curriculum framework to a sufficient degree. In contrast, our goal in identifying the 4DEE elements in assessments was to describe the degree to which these elements are currently used, not to construct a standard for inclusion. Our interpretation of how deeply these elements are used in learning came instead in our next cycle of coding, in which we identified the level of integration between co-occurring elements.

Distinction of Low and High Integration Questions

Our second cycle of coding distinguished between contextual units (i.e., assessment questions) in three categories: no integration, low integration, or high integration. "No integration" questions were those in which all assigned codes were for elements that came from the same 4DEE dimension. The distinction between low and high integration was made with references to interdisciplinary theory. Several scholars of interdisciplinarity have distinguished between the deep integration of interdisciplinary work as compared to the superficial association of disciplines in multidisciplinary teaching and research approaches. For example, while interdisciplinarity is "always transformative in some way, producing new forms of knowledge in its engagement with discrete disciplines," multidisciplinary is only "the simple juxtaposition of two or more disciplines, a relationship of proximity with no real integration between them" (Moran 2010). This distinction has also been described as the difference between interdisciplinarity, in which different ways of knowing are held in relationship, developing over time into the establishment of common ground, larger insight, or deeper understanding of differences, as opposed to multidisciplinary, which is simply knowing about something in two or more ways (Dreyfuss et al. 2011). With slightly more specificity, one scholar noted that interdisciplinary work creates products, solves problems, and offers explanations of the world, while multidisciplinary work, regardless of its goals, does not consider how contributing disciplines are related to one another (Boix Mansilla et al. 2000).

This range of definitions for inter- and multidisciplinary work illustrates the challenge of pinning down specific and replicable criteria for identifying the amorphous phenomenon of interdisciplinarity, let alone integration. To establish criteria that were easier to assess, we used Pauley et. al.'s Continuum of Disciplinary Melding, which defines intra-, cross-, multi-, inter-, and transdisciplinarity and places them in that order on a continuum (Pauley et al. 2019). We further chose to use the 4DEE dimensions as imperfect proxies for disciplines, rather than tease apart the different disciplines represented among elements in each dimension. We established cross- and multi-dimensional questions as "low integration," in which elements from different 4DEE dimensions overlap but can be understood independently of one another. Examples of no integration and low integration questions are provided in Appendix B. Next, we established inter- and trans-dimensional questions as "high integration," for which elements in one dimension needed to be understood in the context of an element from a different dimension, building toward some emergent understanding. For example, if an assessment question provided students with life history data and asked them to run a statistical test on them, that question would be coded for both the life history element in the Ecological Concepts dimension and the statistics element in the Ecology Practices dimension. Since students were asked to use the tools (statistics) from one dimension to answer a question about (life history) data, this question would qualify as a low integration question—it did not particularly matter that the data were about life history. However, if the question asked students to explain *how* the results of that statistical test led to conclusions about life history data, it would be coded as high integration, because students would have had to understand enough about life history and statistics to be able to explain why they integrate in a particular way. In short, the distinction is that high integration questions assessed whether students know *how* or *why* the concepts from the two (or more) different dimensions matter to one another. In contrast, low integration questions presented information from two different dimensions and may have asked students to use it, but do not ask students to identify or explain why that information is relevant.

Distinguishing between low and high integration questions was fairly straightforward for elements in the Ecology Concepts, Ecology Practices, and Human-Environment Interactions dimensions. However, establishing a level of integration for questions that contained Cross-cutting Themes was more complex. Specifically, the complexity came from determining the level of integration for the elements structure and function, pathways of transformation of matter and energy, systems, stability and change, and scales. These themes originated as “big ideas in ecology” (Prevost et al. 2019) and ecologically related ideas that may relate to other areas of science but are not easily sorted into the other three dimensions (Berkowitz et al. 2018). Since these themes came from ecology, establishing how well they integrate with an element of Ecology Concepts is a logically circular task—the themes are only included in the first place *because* they are strongly related to ecology concepts. Cross-cutting themes thus had their own criteria for high integration (with the exception of the evolution and biogeography elements, which were easier to distinguish from Ecology Concepts elements). These criteria were that either the question could be asking students something about the cross-cutting theme on a meta level (e.g., “Why would someone describe the flow of energy between trophic levels as a pathway?”), or the question could be identifying other natural science disciplines that the theme “cut across” in addition to ecology (e.g., “How is the structure-function relationship in a chemical reaction similar to that in an antelope herd?”).

Themes Within High Integration Questions

In the third cycle of coding, we described high integration questions with inductive codes, which are codes not taken from a source reference, but those that emerge in iterative readings of the study documents (Mihas and Odum Institute 2019). These inductive codes were grounded in Nikitina's Three Strategies for Interdisciplinary Teaching (Nikitina 2006). Nikitina's three strategies are "Contextualizing," "Conceptualizing," and "Problem-Centring." In short, Contextualizing is teaching information from one discipline in the context of relevant content from another, for example studying natural selection by explaining the historical context of Darwin's *The Origin of Species*. Conceptualizing means identifying similar mathematical or empirical patterns across disciplines, for example exploring exponential growth as both a mathematical function and a pattern of population growth in living organisms. Problem-Centring is using a range of disciplinary tools to propose a solution for an urgent and real problem, such as proposing a strategy for environmental justice with information from both soil chemistry and sociological explanations of racism. The codes that emerged in this cycle embedded Nikitina's ideas into the specific context of our ecology assessments. These codes are hereafter called emergent themes and are presented in the Results.

Results

Survey Response Characteristics

Our survey was accessed 83 times. Thirty-seven respondents answered at least some questions in the survey and 26 uploaded documents for content analysis. Respondents were instructed to fill out separate surveys if they wished to upload content for separate courses (one respondent did this for three courses). Survey response data are summarized in Figure 1. Of the included courses, the majority were Ecology courses housed in Biology departments at R1

Universities or Liberal Arts Colleges. Respondents were also asked to identify if their university was a Historically Black College or University, a Hispanic-Serving Institution, a Tribal College or University, a Native American Non-Tribal Institution, a Minority Serving Institution, an Alaskan Native- or Native Hawaiian-Serving Institution, an Asian American- and Native American Pacific Islander-Serving Institution, or a Predominantly Black Institution. None of the instructors

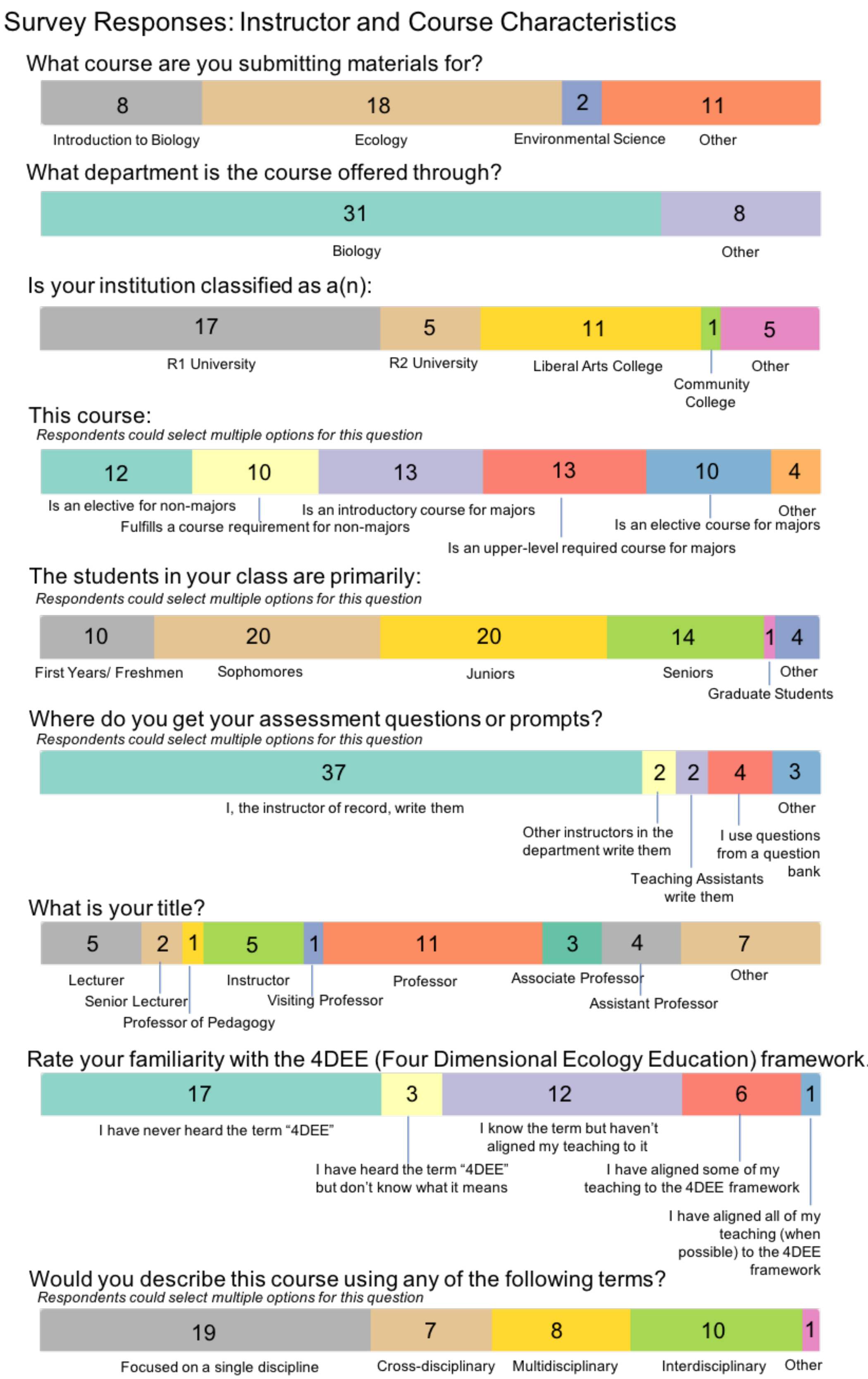

Figure 1: Characteristics of the courses that our study assessments came from.

who uploaded course documents identified their university as belonging to one of these classifications, possibly because we did not specifically target these universities. Several courses were centered around subdisciplines of ecology (e.g., Ecosystem Ecology or Tropical Ecology). The majority of respondents noted that they wrote assessment questions themselves, not sourcing them from a common pool (e.g., a test bank or other instructors). A large majority of courses had been taught for several years (>3 years) by instructors with several years of teaching experience (>3 years). The majority of courses were not aligned with the 4DEE framework. Instructor's self-identification of degree of integration in their courses varied: the most common course description was that the course covered content in a single discipline, but several respondents described their course as interdisciplinary. The exact wording of the survey questions is included in Appendix A.

4DEE Elements

Nearly all elements of the 4DEE framework were identified in our study documents. The prevalence of each element in our study documents is listed in Appendix C. Elements from the Ecology Concepts dimension were coded most often. All elements of the Ecology Concepts dimension were coded at least once. Elements in the Ecology Practices dimension were the next most prevalent codes, though in this dimension, both the informatics and habitat assessment elements were never coded in our study documents. This gap in 4DEE coverage is not surprising, given that the 4DEE elements were never intended to be a required list of coverage for all courses, and indeed some elements may be more relevant to professional certification in ecology-related fields rather than coursework (Berkowitz et al. 2018). Cross-cutting Themes elements were the next most prevalent. Though the parent code spatial and temporal elements was never coded, its sub-elements (evolution, biogeography, stability and change, and scales) were identified fairly frequently.

Integration of Elements Across Dimensions

The vast majority of contextual units were coded for elements in multiple dimensions: of 513 total contextual units in our study, 185 (36%) were coded for elements only in one dimension, 163 (32%) for elements in two dimensions, 119 (23%) for codes in three dimensions, and 45 (9%) for codes in all four dimensions. The most common co-occurrence of dimensions was Ecology Concepts and Ecology Practices, followed by Ecology Concepts and Cross-cutting themes. The Human-Environment Interactions dimension was least often represented in partnerships with the other dimensions. The elements that were most frequent among dimension pairings are presented in Table 1.

High Integration Questions

High integration assessment questions not only elicited elements of multiple dimensions, but they called on these elements in such a way that answering the question required consideration of how elements in different dimensions interacted; a student would be unlikely to answer the question correctly if they divided subject matter from different dimensions and considered each dimension independently. These questions came from a variety of types of assessments, though most came from assessments where students constructed a response than those in which students selected a response. Specifically, 8% of high integration questions came from exam multiple choice questions (selected response) in contrast to the categories of constructed response questions: 54% short answer exam questions, 4% exam essays, 14%

Table 1: Co-occurrences between dimensions in assessment questions in study documents.

A co-occurrence between two dimensions is not exclusive; the same assessment question may also be coded for elements from a third or fourth dimension. Each dimensional pairing is presented with the most common elements from each dimension that appeared in that pairing. Most common elements were those which occurred with frequency in the 90th percentile, relative to all other elements of that dimension.

	Ecology Concepts	Ecology Practices
Co-occurences	1019	
Most common elements that co-occurred with the other dimension		
	biodiversity habitat and niche resources and regulators	arguing from evidence
	Ecology Concepts	Cross-cutting Themes
Co-occurences	1052	
Most common elements that co-occurred with the other dimension		
	competition, mutualism, predation habitat and niche resources and regulators	pathways of matter and energy
	Ecology Practices	Cross-cutting Themes
Co-occurences	493	

Most common elements that co-occurred with the other dimension		
	arguing from evidence	systems
	Ecology Concepts	Human-Environment Interactions
Co-occurences	400	
Most common elements that co-occurred with the other dimension		
	global climate change	climate change
	nutrient cycles	
	biodiversity	
	resources and regulators	
	Ecology Practices	Human-Environment Interactions
Co-occurences	256	
Most common elements that co-occurred with the other dimension		
	communicating and applying ecology	climate change
	Human-Environment Interactions	Cross-cutting Themes
Co-occurences	189	
Most common elements that co-occurred with the other dimension		
	climate change	pathways of matter and energy

research papers, 15% lab reports or post-lab presentations, 4% question sets, and 1% projects. The majority of courses that our study documents came from contained at least one assessment with high integration questions. The most common elements from each dimension that were highly integrated within a question are summarized in Table 2. The elements in this table highlight how many of these high integration questions focused on elements with direct relevance for human well-being, including biodiversity, communicating and applying ecology, climate change, and biogeography (as it relates to invasive species).

Table 2: Three 4DEE elements from each dimension that were coded most frequently among high integration questions.

"Ecology in this course" is not a 4DEE element, but a catch-all code for the ecology concepts dimension, used most often when an assessment question asked students to identify any ecology topic that had come up in that course. Note that a single high integration question could be coded for multiple elements of the same or different dimensions, so quantities displayed here are not mutually exclusive.

Dimension	**Element**	**Number of times coded in high integration questions**
Ecology Concepts	ecology in this course	15
	community\biodiversity	11
	ecosystem\nutrient cycles	10
Ecology Practices	communicating and applying ecology	11
	investigations\experimental design	9
	quantitative reasoning\statistics	4
Human-Environment Interactions	human-accelerated change\climate change	18
	resource management\conservation biology	14
	resource management\agricultural ecosystems	7
Cross-cutting Themes	spatial and temporal\evolution	16
	spatial and temporal\biogeography	9

	pathways of matter and energy	6

Themes Within High Integration Questions

Analyzing the high integration assessment questions led to the identification of seven emergent themes that described categories of how integration was accomplished in these assessments. They were: *Addressing Problems in the Environment*, *Addressing Problems of Racism*, *Emergent Patterns in the Natural Sciences*, *Tailoring Practices to Research Questions*, *Contextualizing in the Humanities*, *Justifying Ecology in Society*, and *Connecting Ecology and Evolution*. Relationships between the themes and Nikitina's Contextualizing, Conceptualizing, and Problem-Centring are summarized in Figure 2.

There are some differences between Nikitina's categories of interdisciplinary teaching and our categories of high integration assessment questions that emerged as the themes listed above. One reason for these discrepancies was a difference in scale between Nikitina's study and ours. Nikitina studied entire, dedicated interdisciplinary programs. In contrast, our study assessments came from single courses without collaborators from external disciplines. We thus established high integration themes that are less aspirational than some of Nikitina's interdisciplinary categories. For example, while Nikitina's Problem-Centring category requires that students attempt to solve a real-world problem, our two *Addressing Problems* categories contain questions in which students only need to understand a problem, not try to solve it. Another difference between our classifications and Nikitina's was the modification we made to suit our specific focus on ecology courses. For example, in our *Contextualizing in the Humanities* theme, we specified that questions must obviously reference a specific discipline in the humanities. This specification was largely a practical modification, as ecology instructors were likely to be trained in the natural sciences and may not be well-versed enough in the humanities to recognize (or replicate) assessment questions that reflect the epistemological goals or research methods of humanities disciplines unless the discipline itself is either explicitly named (e.g., “the history of modern synthesis” or “literature about the tropics”) or reasonably evident. Finally, our focus on ecology meant that some of our themes present interdisciplinary relationships that touch on more than one of Nikitina’s categories. For example, *Connecting Ecology and Evolution* could be done by connecting those two fields through quantitative relationships (similar to Nikitina’s Conceptualizing) and through shared history and philosophy (Nikitina’s Contextualizing). Although our emergent codes did not entirely fit into Nikitina’s three categories, they were established in reference to Nikitina’s theory because her theory is useful for making predictions about the strengths and weaknesses of different approaches, as we do in the Discussion.

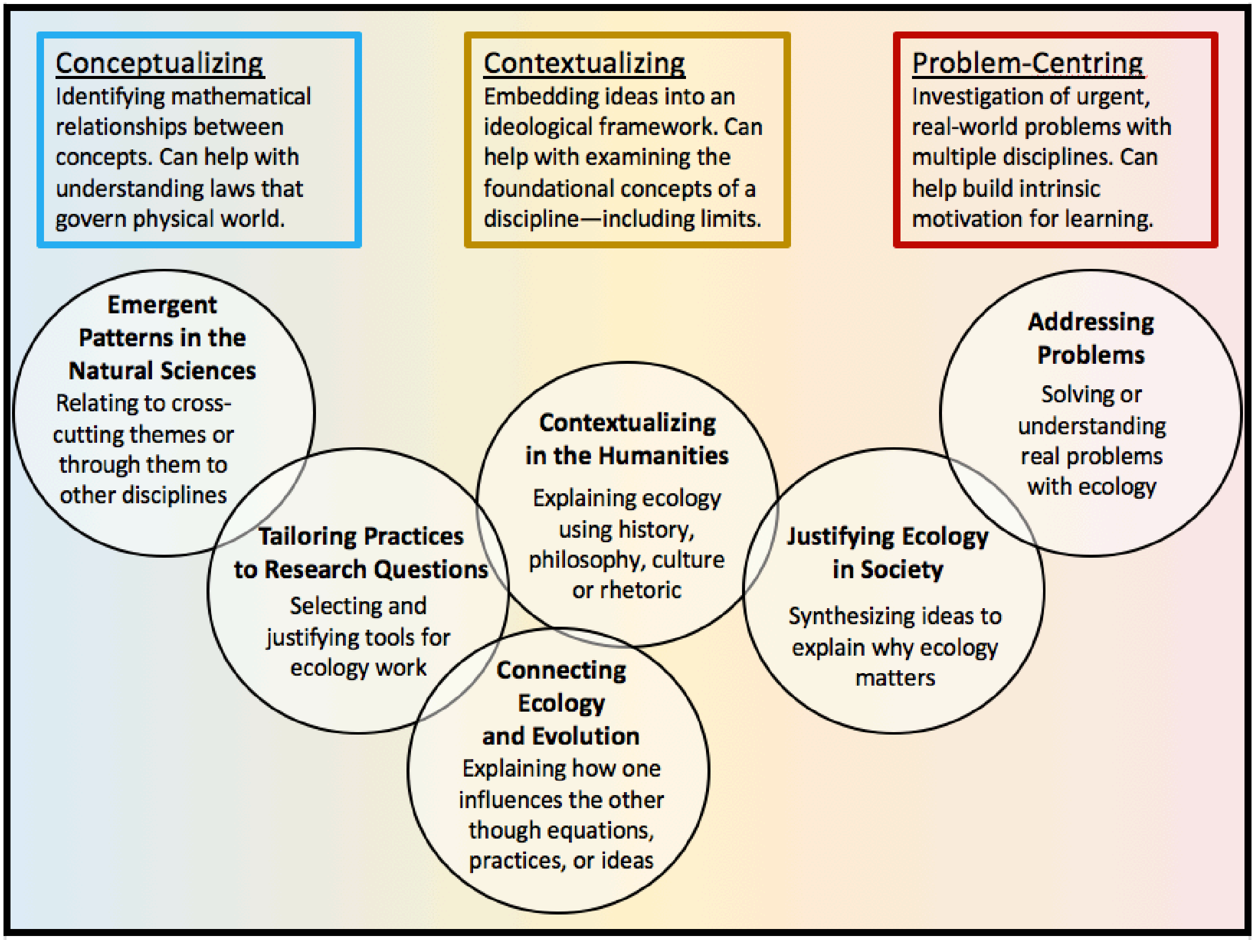

Figure 2: Relationships between high integration themes from this study.

Themes (in circles) are organized by similarity to Nikitina's categories of interdisciplinary teaching (in rectangles).

Emergent themes of high integration assessment questions are described in the following subsections with a summary of the elements they contain and examples of questions that elicited these themes. Example questions from our study documents are presented below for each theme with a brief note about the context of their assessments and the 4DEE elements they were coded for. Example questions are included with permission from the instructors, who requested that we share their course content either with attribution or anonymously. We chose example questions that were relatively concise and easy to understand without the full context of the assessment, that exemplified various characteristics of the theme, and, if possible, came with answers written by the instructors. Some examples are slightly modified to provide additional context (in brackets) and for consistent formatting. We did not fix unconventional grammar or spelling in the questions as provided, in order to present them as students would have seen them.

1. Addressing Problems in the Environment

Questions within this theme asked students to consider how ecology concepts and practices contribute to understanding either an environmental problem or its solution. The question had to ask about a problem that really exists in the world and has had significant impact. Questions about *Addressing Problems in the Environment* involved integration of the 4DEE dimension Human-Environment Interactions. Specifically, the most common problems addressed in our study related to climate change, conservation biology, and agriculture.

Examples of Addressing Problems in the Environment

> Your friend tells you that now that there are [non-native burrowing] rats in the park - they are also thinking about releasing their pet rats in Jubilee Park so that they can be free. As an ecologist-in-training, do you agree or disagree with their idea of releasing their pet rats? Explain **two** reasons to defend your choice.
>
> *Anne McIntosh, University of Alberta*

The above question came from a set of related questions in a final exam in an Ecology course. This question was coded for ecology in this course, because the student was prompted to answer from the perspective of an ecologist, but specific elements of the Ecology Concepts dimension were not mentioned in the prompt. This question was also coded for the 4DEE Cross-cutting Theme element biogeography (because it asked a question about non-native species) and the Human-Environment Interactions elements conservation biology and ethics. This question fit the criteria for high integration because students were asked to explain how biogeographical distribution has specific ecological and ethical implications in this context.

Imagine that a conservation group sells a bumper sticker with the words “save the bees:” Apply the ideas of biodiversity and ecosystem service in your answer. Be as specific as you are able to be.

What are they most likely referring to? Which bees? (1 point)

Answer[provided by instructor]: They can say a specific species (e.g., mason bees), “wild bees,” or domesticated honey bees. It does not matter, as long as they are ALIGNED with part B. If they talk about mason bees here and honey bees below, they do not get this credit.

Why should we save these bees? You only need one, specific answer. It is acceptable to write about a case study (specific example).

Answer[provided by instructor]: We should save bumblebee species, because bumblebees are really great pollinators of plants in the nightshade family that produce food that we eat, such as tomatoes, eggplants, and peppers. Bumblebees live in the natural environment (usually nesting in rodent burrows and nests) and provide us all with the necessary pollination to make the fruits that are the staples of many dishes, including Italian and Mexican ethnic cooking. Though there are other wild pollinators, losing bumblebee species from a community will lower the pollination rate and fruit set of these nightshade-family plants.

Laura Eidietis, University of Michigan

The above question was a standalone question set in a unit exam for a first-year course in a Biology department. The question set was coded for high integration of the Ecology Concepts element biodiversity, the Ecology Practices element communicating and applying ecology, and the Human-Environment Interactions element ecosystem services. This question was also coded for low integration of the elements systems, agricultural ecosystems, and human-accelerated change. This question was identified as high integration because it asked students to use ecological content knowledge to interpret a piece of science communication and explain why this communication matters.

> As climates rapidly warm and optimal habitats shift to higher latitudes, plant species must shift their geographic ranges to keep up. Which types of plants are more likely to keep up, early-successional species or late-successional species? Explain your answer. (Note: This is not asking about primary succession because the areas already have vegetation.)
>
> *Survey respondent requested that their course materials be shared anonymously*

The above question was included in a unit exam in an Ecology course. The question was coded for high integration for the Ecology Concepts element succession, the Human-Environment Interactions element climate change, and the Cross-Cutting Theme element biogeography. This question was coded for low integration of the elements global climate change, habitat and niche, latitude and elevation, gradients, and stability and change. This question was also coded for the high integration theme *Emergent Patterns in the Natural Sciences* because of its integration of biogeography. This was a high integration question because it not only tested students' knowledge of succession but asked them to explain why climate change had different effects on succession depending on patterns of biogeography.

Based on your understanding of successional processes, support your perspective on whether and how this land use change (42% reduction in cropland as beans replace beef) would influence CO_2 emissions.

Answer[provided by instructor]: During succession, biomass, species richness, and nutrient use efficiency tend to increase and then plateau, while productivity may increase and later decline. The build-up of biomass through succession sequesters carbon, and any net positive productivity in late succession continues a net uptake of CO_2*. Agricultural land is kept in any early-successional state. If agricultural land is no longer needed to produce beef, then it follows secondary succession. Plant biomass builds up on late-successional wild land vs crop land, with a net uptake and sequestration of* CO_2*. (3 pts – note that some people also mentioned that beans are plants and take up* CO_2*, whereas cows are heterotrophs and release* CO_2*. While accurate, it does not account for the main land use change, which is not from growing cows to growing beans, but from growing cows to not needing agricultural production from those lands.)*

Survey respondent requested that their course materials be shared anonymously

The above question was taken from a question set in an exam for an Ecology course. This question was coded for the high integration of the Ecology Concepts element succession and the Human-Environment Interactions element agricultural ecosystems. It was high integration of these elements because students were asked to use their knowledge of succession to explain how different agricultural practices influence ecological processes.

2. Addressing Problems of Racism

As in *Addressing Problems in the Environment*, questions in this category prompted students to consider how ecology concepts and practices contributed to understanding real-world problems and solutions, though this theme was specific to content about racism. In our study, questions in this category addressed 4DEE elements environmental justice and biodiversity. Instructors could also use questions in this category to integrate elements such as ethics, environmental philosophies, stewardship, agriculture, and toxicology.

Though questions in *Addressing Problems of Racism* also touched on information about the environment, this theme was separated from the one above because we believe that lessons about racism and ecology create unique pedagogical opportunities (described further in the discussion section) and because previous ecology instruction has not typically focused on the effects of historical and contemporary white supremacy on ecological theory, practice, and significance.

Examples of Addressing Problems of Racism

> Whether in our study or from patterns in the literature, variation in the ecology of urban environments has important effects on people. Here we are not thinking of the drivers (=causes) of the patterns in data, but rather the consequences of these patterns. Why do these correlations matter? Consider the effects of having fewer trees, or more impervious surfaces, or less access to green space. The word “heat island” should appear somewhere, among topics.
>
> *Survey respondent requested that their course materials be shared anonymously*

The above question was taken from prompts for the discussion section of a report students were instructed to write after a crosstown walk exercise about the correlation between socio-economic and ecological factors. It was coded for a high integration of ecology in this course and the Human-Environment Interactions element environmental justice. This question was high integration because it asked students to explain how ecology patterns affect people in different ways based upon social factors like environmental justice (or a lack of it.)

3. Justifying Ecology in Society

Questions that were categorized as *Justifying Ecology in Society* asked students why ecological concepts were relevant to human concerns. To answer these questions, students had to synthesize their knowledge of ecology with their understanding of society, as influenced by their own experiences or their knowledge of ethics, politics, economics, and culture.

Questions in this category often shared the identification of real-world problems that was common to questions in both of the *Addressing Problems* themes. Indeed, *Justifying Ecology in Society* questions were another opportunity for instructors to link the 4DEE Human-Environment Interactions dimension to the other three dimensions. However, in contrast to *Addressing Problems*, questions in this category did not provide a problem to apply ecology to; instead, students were given an ecology concept (or asked to identify one) and explain why it mattered. This distinction between *Addressing Problems* and *Justifying Ecology in Society* perhaps mirrors the approaches of applied versus basic research, respectively. In support of this distinction, several questions in this category presented students with a hypothetical funding source and asked students to justify which research projects they would allocate it to.

Examples of Justifying Ecology in Society

Research Topic Description

• Pick any ecological topic that is both important to the society and interesting to you.

• Explain (a) the concept and (b) its major components in the first paragraph

• Identify (a) its significant implications under current anthropogenic changes and (b) major controversies involved in the scientific literature

• Cite 2-3 references (primary research or review papers) that you plan to read further for the topic (this is optional, but will be very helpful for me to understand your topic)

Survey respondent requested that their course materials be shared anonymously

The above prompt comes from the proposal component of a research paper and presentation in an Ecology course. It was coded for the high integration of ecology in this course and the Human-Environment Interactions elements human-accelerated change, resource management, ecosystem services, and ethics (while a student may have been unlikely to cover all of these elements, the prompt seemed to direct students toward at least one of them.) This was a high integration question because students are asked not only to describe ecology concepts but also how this concept is affected by (or affects) human actions.

If you were in charge of the provincial budget and you had 1 million dollars that you could provide to University of Alberta researchers in order to help improve our understanding of ecological interactions, what would be your top three ecological research priorities for allocating this money? Provide thoughtful reasons for selecting these areas for research.

Anne McIntosh, University of Alberta

The above question was taken from a final exam in an Ecology course. It was coded for the high integration of ecology in this course and the Ecology Practices element communicating and applying ecology as well as the Human-Environment Interactions elements human-accelerated change, resource management, ecosystem services, and ethics. Again, students would be unlikely to integrate all of these latter elements, though it seems likely that at least one of them would appear in a student's thoughtful reasoning. This was a high integration question because students are asked to use one of the Human-Environment Interactions elements to explain why a particular ecology concept is valuable to a specific audience (the provincial government) that is likely to have specific application goals (even for basic research).

4. Contextualizing in the Humanities

Questions in this category asked students to humanize their knowledge of ecology by explaining some aspect of ecology in the context of philosophy, religion, history, languages, linguistics, literature, or the arts. *Contextualizing in the Humanities* was another source of connection to the 4DEE Human-Environment Interactions dimension, though this theme wes also well equipped for close examination of elements in Ecology Concepts, Ecology Practices, or Cross-cutting Themes.

Contextualizing in the Humanities shared conceptual overlap with *Justifying Ecology in Society*. However, they were distinct in that the goal of questions in *Contextualizing in the Humanities* was for students to analyze what ecology *is*, whereas in *Justifying Ecology in Society*, students were asked to make a value judgement about what ecology can *do*.

Examples of Contextualizing in the Humanities

Explain the mechanisms (=causes) for the patterns described above.

A. What do our data tell us about the relative shade tolerance of the common species in our forest plots? Notice how we learn something about tree physiology just by counting trees!

B. Clarify how shade tolerance explains why some species are increasing and others are decreasing.

C. What historical factors may also contribute to the reasons some species are either increasing or decreasing in our forests? Relate your knowledge of New England history at a very simple level. Hint: why are there stone walls throughout our forests?

Answer[provided by instructor]: Species are decreasing because they have low shade tolerance. Few oaks and pines survive as small trees in the shade of larger trees, including shade from adults of their own species. Aspen and (White birch, FYI) do not even have ANY saplings at all, showing they have the lowest shade tolerance of all. In contrast, the species that are increasing all have high shade tolerance. These patterns are due to the history of this land. The abundance of Oak and Pine, and the presence of Aspen, suggest the area had been open and sunny at some point. In this case, the stone walls suggest this was agricultural land, probably grazed for sheep or cattle. Then the forest started to move in 100-150 years ago. The first species to take over are those who make up the large trees today, but they are starting to be replaced by more shade-tolerant species.

Survey respondent requested that their course materials be shared anonymously

The above question set came from a list of questions that followed a session of data collection in the field in an Ecology course. This question was coded for high integration of the Ecology Concepts element biodiversity and the Human-Environment Interactions element agricultural ecosystems. This was a high integration question because students were asked to explain how historical patterns of human activity influence current ecology.

> I have tried to get you to think of “schools of Ecology” as being organized along the lines of “determinism” vs “probabilism” “Open systems” vs “closed systems”. Identify the key exponents of each school. Explain in your own words why you place particular researchers in a particular “school”. How do these schools differ from each other in assumptions? In methodologies?
>
> *John Anderson, College of the Atlantic*

The above question was included in a list of potential prompts for which students were assigned to write a five-page research essay. This question was coded for the high integration of ecology in this course, the Ecology Practices element experimental design, and the Human-Environment Interactions element environmental philosophies. This was a high integration question because students were asked to directly explain how differing philosophies drove groups of ecologists to different research methodologies.

> Discuss how concepts of “balance” “stability” and “order” presented in the first half of the term creep into popular literature such as Leopold’s *sand county almanac,* John Steinbeck’s *Log from the sea of Cortez,* and other non & quasi-fictional works. Trace

> these ideas from pre-ecological origins, including reference to theology & philosophy. This is intended as a "thought question" & is perhaps more for those of you less "into" the Hard Science part of the course, but I expect you to be rigorous & find clear evidence for your positions!
>
> *John Anderson, College of the Atlantic*

The above question also came from a list of potential prompts for which students were assigned to write a five-page research essay in an Ecology course. This question was coded for the Ecology Concepts element stability and disturbance, the Ecology Practices element communicating and applying ecology, the Human-Environment Interactions element environmental philosophies, and the Cross-cutting Theme stability and change. This was a high integration question because students were prompted to describe how a specific genre of science communication (fiction) interprets ecological concepts (which fit into a broader theme in multiple natural sciences) through the lens of a particular philosophical perspective.

5. Connecting Ecology and Evolution

This theme included a specific group of assessment questions that contextualized ecology in either evolutionary theory (e.g., that there are ongoing interactions between evolutionary and ecological processes) or evolutionary history (e.g., that ecological interactions exist today as a result of evolution in the past). The narrow scope of this category made for obvious connections to the 4DEE element evolution in the Cross-cutting Themes dimension.

Examples of Connecting Ecology and Evolution

> Common plantain (Plantago major) growing along paths or in trampled area have small leaves and short flowering stalks; common plantain growing in undisturbed, unmowed fields have long leaves and long flowering stalks. How much of this variation is due to genetic or environmental modification? Outline an experiment to answer this question.
>
> *Andrea Worthington, Siena College*

The above question was taken from a final exam in a plant ecology course. It was coded for high integration of the Ecology Concepts element habitat and niche and the Cross-cutting Theme Evolution. It was also coded for the low integration of experimental design and structure and function. This was a high integration question because it asked students to explain how genetic modification (evolution) affects (or does not affect) a plant differently in two different ecological scenarios.

> Edith's checkerspot is a butterfly that lives in western North America. Populations are very isolated, as this butterfly seldom flies very far. Each population is a specialist, using a particular type of plant for laying eggs. Whether we personally care very much about this tiny animal, it can teach us a lot about biology. Picture a population of Edith's checkerspot butterflies that is isolated enough such that migrants from only populations only get there sometimes once per year when strong winds blow from the deserts to the east. Some years there are no migrants.

What is one way in which humans can affect the evolution of animals? Answer using Edith's checkerspot butterflies as an illustrative example. Be very specific.

Answer[provided by instructor]: Evolution: descent from an ancestor with genetic modification from that ancestral state; this can mean modifications within a species or population AND the origin of new species from ancestral species

A population of Edith's checkerspot butterflies lived in a meadow in Nevada. They used blue eyed Mary as a host plant for laying eggs. Almost all the butterflies did this – they were specialists on blue eyed Mary. Humans changed the environment when they brought cattle into the meadow. Blue eyed Mary died off, and there was a lot of plantain. Plantain was different, in that it was around for more of the year, potentially expanding the breeding season of the Edith's checkerspot. The problem was that almost all the Edith's checkerspots would not use plantain, so they died without progeny. A few Edith's checkerspots were able to use the plantain. They lived and had a lot of offspring, passing their ability to use the plantain on to their offspring. Maybe some of the offspring did not inherit this ability and died without offspring, but a lot lived and reproduced. This, in and of itself was evolution, but we didn't know it, because we didn't know if the host-plant choice was genetic or something that was plastic. We found out. When the humans moved the cattle out, the blue eyed Mary came back. But, the butterflies left in the meadow could not use the blue eyed Mary anymore - the alleles for using that plant must have been purged from the population during the plantain dominance years. This indicates that the change was a genetic change.

Laura Eidietis, University of Michigan

The above question is from a unit exam in a first-year biology course that was coded for the Ecology Concepts element life history, the Human-Environment Interactions element human-accelerated change, and the Cross-cutting Themes element evolution. This question was also coded with the high integration theme *Addressing Problems in the Environment*. This question was high integration because students were asked to explain how humans can influence evolution, and why this matters to the life history of a particular insect.

> How has Ecology been influenced by Evolutionary Biology/Darwinism? Has it? Where do you see possible synergies/conflicts between Darwinian thought and ecological ideas?
>
> *John Anderson, College of the Atlantic*

The above question came from a list of prompts students were directed to choose from to write a research paper in an Ecology class. This was coded for high integration of ecology in this course and the Cross-cutting Theme evolution because students are directly asked how one influences the other.

> What is co-evolution? How do you demonstrate it? When is it likely to occur? How might ideas of co-evolution feature in notions of ecosystem ecology? What sort of evidence would you look for in invoking co-evolutionary explanations for ecological outcomes?
>
> *John Anderson, College of the Atlantic*

The above question also came from a list of prompts students were directed to choose from to write a research paper in an Ecology class. This question was coded for high integration of the Ecology Concepts element ecosystems and the Cross-cutting Theme evolution, again because students are asked how these elements influence one another.

6. Tailoring Practices to Research Questions

In this theme, assessment questions asked students to explain how or why an ecology practice applies to the study system or ecological concept of inquiry. Thus, questions in this category were likely to integrate 4DEE elements in Ecology Concepts and Ecology Practices. To answer these questions, students would consider both their knowledge of the ecology concept *and* the practice to justify why they are well suited to one another. Some content and practices were related by equations, the structure of data, or other quantitative relationships. However, other concepts and practices were related by social conventions (such as the communicating and applying ecology element of Ecology Practices) and interpersonal relationships (such as the collaboration element of Ecology Practices).

Examples of Tailoring Practices to Research Questions

Which ecological relationships are easiest to observe in the field?

Anne McIntosh, University of Alberta

The above question came from one of the "guiding questions" that were to be assessed in a presentation following a lab activity in an Ecology course. While this question did not directly ask students to explain their answer, this was a high integration question because it prompted students' consideration of *how* different ecological interactions apply to their field techniques.

This question was coded for the high integration of Ecology Concepts element competition, predation, mutualism and Ecology Practices element fieldwork.

> What do the patterns in our graphs tell us about diversity in this stream and pond? In which habitat is diversity higher, and how do you know from the graphs? Warning: you made two graphs in this lab, so discuss both graphs thoroughly. Including a little data helps, too.
>
> Answer: *Rank-abundance graph: There were 25 species in the pond but only 21 in the stream. Evenness (slope) was about the same in both habitats (or maybe slightly higher evenness in pond, but only slightly).*
>
> *Survey respondent requested that their course materials be shared anonymously*

The above question came from a set of questions following a lab exercise in an Ecology course. This question was coded with high integration of the Ecology Practices element data skills and the Cross-cutting Theme biogeography because students were asked to describe why features of a data visualization led to certain ecological conclusions.

> Justification – linked back to Research brief where appropriate.
>
> Does the exhibit include opportunities for environmental or educational enrichment?
>
> Is the space functional, safe, and does it mimic the animal's natural habitat?
>
> Does the space include engaging interpretation and a creative use of space for viewing opportunities?

Conservation Connection: How does the solution/process connect to conservation efforts? What is the conservation story that can be shared with guests? What does exhibit design have to do with conservation?

Zach Grimes, Middle Tennessee State University

The above question came from a project in which students proposed a design for an animal enclosure in a zoo for a teacher education course. This question was coded for high integration of the Ecology Concepts element habitat and niche, the Ecology Practices element communicating and applying ecology and the Human-Environment Interactions element conservation biology. These elements were considered highly integrated because students were asked to consider how ecological factors in the exhibit influence communication to a specific audience and why this matters to conservation efforts.

The logistic equation has served as the basis for a wide array of ecological models. Deconstruct the equation for me, showing what assumptions are built in to the idea, where Biology might play a role, what sort of measurements might be needed to apply a logistic model to population growth, where potential errors and abuses might creep in. Why is the logistic such a popular tool in resource management?

John Anderson, College of the Atlantic

The above question came from a list of prompts students were directed to use to write a research paper in an Ecology course. This was coded for high integration of the Ecology Concepts element growth curves, the Ecology Practices element quantitative reasoning, and the Human-

Environment Interactions element resource management because students were prompted to explain how a mathematical model represents an ecological phenomenon and why this matters to resource management.

> Define population regulation. Distinguish (with examples) between intrinsic and extrinsic population regulation. Are all populations "regulated"? Why or why not? How might the organism that you study affect your views of "regulation"?
>
> *John Anderson, College of the Atlantic*

The above question also came from a list of prompts students were directed to choose from to write a research paper in an Ecology course. This was coded for high integration of the Ecology Concepts element growth curves and the Ecology Practices element investigations because it asks students why experimental design (specifically, choice of study system) influences conclusions about an ecological concept.

7. Emergent Patterns in the Natural Sciences

Questions about *Emergent Patterns in the Natural Sciences* asked students to connect ecology to other natural science disciplines, either by specifying the relevant discipline (as seen in our third example below) or by connecting an element in Ecology Concepts to one of the elements in the Cross-cutting Themes 4DEE dimension. The elements in Cross-cutting Themes were added to 4DEE in part because of their similarities to other fields of science (Berkowitz et al. 2018), elements that we interpreted to be systems, pathways and transformations of matter and energy, and structure and function. By this logic, assessment questions that explicitly related ecology concepts to one of those cross-cutting themes were connecting this content to overarching scientific concepts. The ubiquity of a concept across several natural sciences is likely to have a quantitative core, such as the mathematical relationship between surface area and volume that defines many structure-function relationships in biology and chemistry.

Examples of Emergent Patterns in the Natural Sciences

> Which type of photosynthetic pathway would you most likely expect the new pin-cushion plant species to have? Provide one reason for your choice.
>
> Compare/contrast this pathway and the other two photosynthetic pathways - explaining two ways in which they are similar and/or different.
>
> Provide an example of a type of habitat or biome where you would expect to find the other two types of photosynthetic pathways.
>
> *Anne McIntosh, University of Alberta*

The above question comes from a question set in a midterm exam in an Ecology course. This question was coded for the high integration of the Ecology Concepts elements biome type and habitat type and the Cross-cutting Theme pathways and transformations of matter and energy because the question elicited this concept of pathways at a meta level by asking students to identify and compare two similar photosynthetic pathways, likely analyzing differences in the transformation of both matter and energy in each.

> Explain (or draw) how the abundant organic carbon stored in soils of northern biomes could be involved in a positive feedback with global warming. Either one of two feedbacks is acceptable. A drawing with arrows is fine, but you must label/explain what each arrow means.

Survey respondent requested that their course materials be shared anonymously

The above question is the first part of a question set in an exam in an Ecology course. This question was coded for high integration of the Ecology Concepts element biome type, the Human-Environment Interactions element climate change, and the Cross-cutting Theme systems, because feedback loops were considered to be a core component of systems in the Vision and Change curriculum framework (Brownell et al. 2014). This was a high integration question because students are asked to explain how a particular biome influences a feedback loop and why this yields climate change.

How have and do ideas about geology and continental drift influenced concepts in ecology?

John Anderson, College of the Atlantic

The above question, which comes for a list of prompts for a research essay in an Ecology course, is an example of a question in *Emergent Patterns in the Natural Sciences* that connects to these patterns by explicitly naming connected disciplines. This was coded for the high integration of ecology in this course and the Cross-cutting Theme biogeography because it asked how various disciplines (including ecology) influence biogeography.

Discussion

We found that the majority of assessment questions in ecology-content courses touched on elements in multiple dimensions of the 4DEE framework. Elements from Ecology Concepts were, unsurprisingly, represented most well often in assessments, followed by those in Ecology

Practices and then Cross-Cutting Themes. Elements from the Human-Environment Interactions dimension were least frequently found in the contributed assessments overall. However, Human-Environment Interactions elements were fairly well represented among high integration questions, occurring nearly as often as elements in Cross-Cutting Themes and more often than those in Ecology Practices. High integration questions not only mentioned multiple elements but asked students how these elements interacted with one another. The majority of high integration questions and activities came from courses that instructors did not consider to be interdisciplinary, a finding that is consistent with both the challenging nature of defining interdisciplinarity (Graff 2016) and the distinction between interdisciplinarity and integration across dimensions discussed in the introduction. We found that high integration questions fell into one of seven theme categories that describe their relationship to the 4DEE framework, their interdisciplinary approach, and their potential benefits and limitations in ecology courses.

Evaluating the Opportunities and Limitations of Each High Integration Theme

Nikitina (2006) identifies both benefits and drawbacks of each of her categories of interdisciplinary teaching. By understanding the benefits and drawbacks of Nikitina's interdisciplinary categories, we can infer some of the potential benefits and drawbacks of the emergent high integration themes that we have identified and their power to help students integrate across dimensions of the 4DEE framework.

Themes Based on Problem-Centring

Problem-Centring lessons offer students relevance and motivation (Nikitina 2006). Students can work to solve problems in lessons to understand their development of academic skills and content knowledge not merely in terms of their individual gain, but as a source of change in their communities. Further, lessons about real-world problems can help illustrate the key ecological principle that some resources are finite, and that over-use of these resources affects ecological processes (Knapp and D'Avanzo 2010). However, Problem-Centring alone does not help students consider *why* they should seek to change their communities nor *how* they should ethically and responsibly engage in different change efforts. In our study, questions in either of the Addressing Problems categories (*Addressing Problems in the Environment* and *Addressing Problems of Racism*) can provide opportunities for students to practice real-world application of their ecological knowledge, though this practice may be infused with students' uninterrogated assumptions about which problems deserve to be addressed and who the solutions should benefit.

1. Addressing Problems in the Environment

Questions within this theme could facilitate student work on interdisciplinary teams, particularly if those questions prompt students to identify not only the strengths of an ecological approach but also its limitations. Identifying the limitations of an ecological approach could help students cultivate "critical disciplinary awareness," an interdisciplinary skill with which students can evaluate the constraints of their own discipline and the complementary advantages of perspectives and practices from other disciplines (Woods 2007). Instructors interested in preparing students for this skill may deepen questions *in Addressing Problems in the Environment* by prompting students to re-complicate a "solved" problem, perhaps asking: Where could your solution go wrong? What would your team need to do to fix it?

However, even after answering these questions, a limitation of this theme is that students would not necessarily be able to explain what they believe their role should be in solving these problems nor why the problem is important.

2. Addressing Problems of Racism

By integrating course studies of racism and ecology, instructors and students have a rich opportunity for better understanding the insidious philosophical and cultural foundations of ecology as a natural science. For example, one ubiquitous ideology in ecology is universalism, which posits that the process of science is unaffected by subjective factors like the identities of scientists; scholars like Dubois Baber use Critical Race Theory to critique this ideology by centering the perspectives on communities of color (Baber 2020). In this example, identifying universalism in science is not simply an esoteric exercise, as universalist constructs like meritocracy and objectivity underlie hierarchies of privilege in predominantly white institutions, empowering white instructors to dismiss the accomplishments of African American, Latino American, and Native American students (Baber 2015). This example illustrates one asset of the theme; by recognizing and critiquing universalist ideology, students may find a deeper understanding of how ecological issues such as environmental degradation are largely shaped by social structures of privilege and power. Previous scholars have outlined how ecology lessons can be enriched by an approach that centers communities of color. For example:

> …climate change is an environmental issue that is widely addressed in scientific research and education for its global impacts. To make a meaningful connection between climate change and community, we can focus on how climate change disproportionately affects marginalized communities (e.g., pollution, food security, extreme weather events) and

> discuss why this makes their input and leadership in research even more valuable. Community-relevant topics can be integrated into the classroom by incorporating the diverse viewpoints and perspectives from historically underrepresented groups into traditional lecture topics (e.g., environmental justice in climate change, subsistence fisheries and food security in fisheries and conservation, Indigenous rights in resource management). (Arif et al. 2021)

Within 4DEE, insights such as Arif et al.'s are essential for discussing elements in the Human-Environment Interactions dimension.

While *Addressing Problems of Racism* can provide opportunities in an ecology course, instructors should be thoughtful in their approach. Lessons and assessments about racism are likely to have personal relevance for students, and instructors should be careful to not reaffirm racist paradigms that harm students of color. Existing research and guidance (Chaudhary and Berhe 2020; Arif et al. 2021; Cronin et al. 2021) can help instructors consider the existing barriers in their courses that create disproportional challenges (and their alternatives) for students who are Latinx (Camacho et al. 2021), Black (Weston et al. 2019; Mills 2020), Asian American (Nguyen et al. 2022), Native American (Bang and Medin 2010; Smith et al. 2014), and, in intersection, LGBTQ (Cooper et al. 2020). This guidance is relevant to our study, as some courses included assessments in which self-identified white instructors asked their students to consider factors of racism and genocide within ecology exams. (Those questions are not included as examples here, as they did not directly touch on multiple elements of the 4DEE framework). While moves toward addressing racism and other forms of structural oppression in ecology courses are laudable, it seems possible that an unexpected question about structural oppression in a timed, high-stakes assessment may create barriers such as stereotype threat (Kellow and Jones

2008), contributing to broader patterns of harm (Fischer 2010; Johnson-Ahorlu 2013), even when the intention is to disrupt those patterns. For example, a student of color may be forced to use exam time to consider if their white instructor will fairly grade an honest response, or if the instructor will consider the student's analysis of their relevant experiences to be "wrong." Of course, in our study, it is impossible to make judgements about the context surrounding these exam questions, including how instructors have prepared students for them during lessons. However, since questions about racism appeared in our study documents, it seems prudent that we consider how these questions may affect students.

In constructing assessments about ecology and racism, instructors, particularly white instructors, should seek to better understand themselves and their classrooms (Dewsbury 2020). For assessments, students may benefit when instructors consider, amongst other things:

- During this assessment, will students have the opportunity to take breaks, using this time to potentially set boundaries or evaluate how the assessment is affecting them (Johns et al. 2008)?
- Do students have a choice on the topics or format of their assessment (Arif et al. 2021)?
- Are students graded in such a way that they are held to a dominant social standard such as white supremacy (Inoue 2019)?
- Does the assessment focus only on the suffering of people of color, or does it highlight their professional accomplishments (El-Sabaawi et al. 2020) or otherwise draw on the cultural wealth (Stanton et al. 2022) of students of color?

Many of these suggestions apply to all assessments, not only to assessments that include questions about racism. Thus, instructor's careful consideration of how to teach lessons about racism is not extra work for teaching an ecology course, but rather an essential component of developing any course that does not disproportionately perpetuate racist harm.

Careful consideration is also important because of an inherent limitation of the *Addressing Problems of Racism* theme, which is that questions in this theme do not necessarily address the historical and contemporary social context that creates racism and makes these problems so important.

Themes Based on Contextualizing

Nikitina (2006) explains that Contextualizing approaches to interdisciplinary teaching can help students question the presuppositions that underlie science, perhaps recognizing how their and others' perspectives shape their observation and interpretation of scientific phenomena. Contextualizing can also offer students new learning tools, as seen in chemistry classes in which students improved their grasp of mathematical relationships using artistic exercises (Bopegedera 2005). However, Contextualizing does not necessarily include learning about specific disciplinary practices and content knowledge and would be a flawed approach for learning something like laboratory techniques. Among our categories of integration, *Contextualizing in the Humanities* and *Justifying Ecology in Society* describe assessment questions that may help students better understand ecology as a discipline. However, this understanding alone is not likely to make them better field researchers.

3. Justifying Ecology in Society

Assessments that ask students to explain why ecology is important allow students to build metacognitive skills, which can increase long term retention of course materials (Spellman et al.

2016). Justifying ecology can also provide intrinsic motivation for learning when students are drawing from their own opinions and experiences. For example, learning and research experiences that align with students' goals and values can help Native American students feel a greater sense of belonging in science and persist in science careers (Chow-Garcia et al. 2022). Further, questions that connect ecology to a moral, philosophical, economic, or political context may present the opportunity for students to interrupt the conventional priorities of Western science and instead root ecology in cultural relevance, such as in Sánchez Tapia et al.'s study of a lesson plan for Nahua middle schoolers in which students were introduced to the concept of natural selection through discussions of selective breeding in local agriculture (Sánchez Tapia et al. 2018).

Instructors can use *Justifying Ecology in Society* questions in assessments to challenge students to demonstrate their understanding of course materials by tying it to personal, cultural, political, or economic relevance. However, if taught alone, a limitation of this theme is that these questions do not necessarily help students develop the ecological skills and knowledge that will be relevant to their lives and careers. For example, through assessments in this theme, a Nahua college student may learn that species identification is a valuable skill she will use in her future career as a doctor. However, she would need to pursue a separate lesson to actually learn to identify the snakes that are likely to bite her patients.

4. Contextualizing in the Humanities

Lessons that place ecology ideas in a humanities context may present students with rich opportunities to learn more about concepts like climate change that they experience both as science content and as a phenomenon with strong impacts on their (and others') lives (Hulme

2011). Questions under this theme may help students identify bias in ecological thought and limitations of ecology as a field of inquiry, particularly if instructors prompt students to identify what topics their course materials *have not* included, and what other disciplinary perspectives could offer. Indeed, ecologists across cultures may need to draw upon historical context to work toward more accurate and justice-oriented ecological work:

> Examining the history and present challenges in the field of conservation provide insight and a way forward in a world which seems to be increasingly more hostile to equity-seeking groups. Conservationists as a group need to contend with their role in actively maintaining a system which rewards privilege and contains multiple barriers for access and full participation by marginalized communities. Developing mechanisms to root out white supremacy and colonial mindsets will question the very foundations of the field and will be among the most challenging and pressing tasks we will face in coming years….In order to understand the contemporary context of ecology and conservation, it is imperative that we look to history. (Chaudhury and Colla 2021)

Another reason this emphasis on history is important for understanding ecology topics is because all ecosystems are influenced by the history of human activities on that land. Knapp and D'Avanzo (2010) identify historical context as one of the key principles of ecological thought, noting that ecological systems are contingent on legacy effects created by previous human actions.

One limitation of this theme is that understanding these contexts does not necessarily guide students in how to use their knowledge in practice. For example, an aspiring researcher may understand the historical connections between imperialism and ecology but not know how this relationship shapes contemporary research questions, practices, and interpretations in their chosen study system.

Themes Based on Conceptualizing

Conceptualizing is an interdisciplinary technique in which students use specific disciplinary practices to simplify data to their mathematical or empirical core (Nikitina 2006). For example, this technique may be approached by lessons in which students simplify a real situation into a mathematical model that they can validate with their knowledge of the real situation (Maass, Geiger, et al. 2019). However, these conceptual connections often require a good deal of instructor guidance (Nikitina 2006) and, even when understood, may have limited significance or personal connection for students. Similarly, our categories of 4DEE integration *Emergent Patterns in the Natural Sciences*, *Tailoring Practices to Research Questions*, and *Connecting Ecology and Evolution* are likely to elicit deep thought about the relationships between the sciences. As a limitation, students may not be likely to initiate these deep thoughts or persevere in understanding the complexities of scientific interrelationships unless they are incentivized to do so and shown why these ideas matter.

5. Connecting Ecology and Evolution

Ecological patterns and processes are constrained by evolutionary history. This concept is a key principle in ecology education, as evolutionary processes can help to explain ecological patterns (Knapp and D'Avanzo 2010). Students who strive to explain the connections between these fields are likely to develop a better understanding of both. Making connections between ecology and evolution can be done by exploring the entwined historical roots of the disciplines (such as foundational contributions by Charles Darwin (Spalding 1903)) and specific quantitative connections (such as those in population genetics).

A limitation of this theme is that students may be able to connect ecology and evolution but not know how to use that information to address problems. For example, a student may be able to identify that natural selection is an important part of disease ecology, but not know how this applies to a real-life agricultural pathogen.

6. Tailoring Practices to Research Questions

Questions in *Tailoring Practices to Research Questions* are well equipped to help students build interdisciplinary skills like conceptual competence, in which they learn to how to appropriately use tools from one discipline to meet goals in another (Woods 2007). Instructors wishing to prompt deeper consideration of questions in this theme could consider a meta approach for upper-level students, perhaps having them categorize different forms of Ecology Practices elements (e.g., different types of statistics tests) according to their suitability for different types of ecological data, or having students investigate to what extent certain ecology practices are used by convention versus evidence-based justifications.

One limitation of this theme is that students are not necessarily asked to investigate the impacts of Ecology Practices in a broader context, such as the environmental damage that has been caused by destructive sampling or the exploitation of colonial relationships in some international field work.

7. Emergent Patterns in the Natural Sciences

Instructors may be able to use *Emergent Patterns in the Natural Sciences* most effectively when they teach students directly about the connections between course materials and relevant cross-cutting themes. For example, lessons or assessments may prompt students to use cross-cutting themes as organizing principles that they sort course content into along with content they know from chemistry, physics, and math classes. This meta-disciplinary approach in which students talk explicitly about disciplines is a useful tool in interdisciplinary teaching (Boix Mansilla et al. 2000). Questions about *Emergent Patterns in the Natural Sciences* can also help students build the interdisciplinary skill of competence in negotiating meaning, which is understanding how key terms in one discipline are defined differently in another, an essential tool for communication in collaborative teams (Woods 2007). However, one limitation of this theme is that questions do not necessarily ask student to explain why those collaborative teams matter or what problems could be solved with collaboration.

Each of the categories we have identified of existing high-integration assessment questions have potentially troubling limitations. Fortuitously, instructors can combine these different approaches to 4DEE integration in order to ameliorate the limitations of any particular high integration theme.

Using High Integration Themes as Building Blocks

One of the inherent boundaries of interdisciplinary teaching is that undergraduate courses tend to have a single instructor, and each instructor has limits on the range of their expertise. For ecology instructors considering the possibilities of integrating across dimensions of 4DEE (and perhaps accomplishing interdisciplinarity along the way), logistical boundaries likely prevent them from covering elements as disparate as informatics or environmental philosophy. A single ecology instructor is unlikely to have the pedagogical training to range too far into other disciplines. Of course, these limitations are acknowledged by the creators of the framework, who clarify that no course needs to cover all elements (Berkowitz et al. 2018; Prevost et al. 2019). However, courses do not exist in isolation: students in ecology-related majors are likely to take many courses in biology and other natural sciences, taught by biologists and other natural scientists, and it is possible that the limits of their instructors' expertise follow common patterns, leaving behind common gaps. Consider, in particular, Human-Environment Interactions. This dimension was the least represented among our study documents. For many of the elements in this dimension, instructor expertise, while certainly possible, is unlikely to come from their training as scientists (relative to their knowledge of the other dimensions). It seems unlikely that an instructor with little training in an element would be able to integrate it into a lesson, applying the appropriate epistemological framework to the appropriate questions and topics. In addition, this problem persists outside of the classroom; these epistemological differences between disciplines—particularly those that researchers are not aware of—can plague multidisciplinary teams (Brister 2016).

Integration across dimensions, then, may have more utility as preparation for interdisciplinarity. Each of the high integration themes we have identified in this study may be most effective when they are combined in sequence with the explicit goal of teaching students what ecology is and also what it is not, so that students understand how ecology fits with other disciplines in advancing scholarship and solving problems. The potential opportunities presented by combining themes in sequence are summarized in Figure 3.

Conceptualization-heavy themes like *Emergent Patterns in the Natural Sciences*, *Tailoring Practices to Research Questions*, and *Connecting Ecology and Evolution* offer deep thinking about science but could improve with pairing with the *Contextualizing in the Humanities* theme. For example, students might be better prepared to evaluate the data that supports ecological concepts if they also understand the ideologies of foundational contributors to statistics (Clayton 2020) or some of the environmental philosophies in the Human-Environment Interactions dimension. In addition, students may find intrinsic motivation to understand the math-heavy concepts that cross sciences if they apply their quantitative skills to socio-scientific problems, in activities such as the conversion of real-life scenarios to mathematical models (Maass, Doorman, et al. 2019).

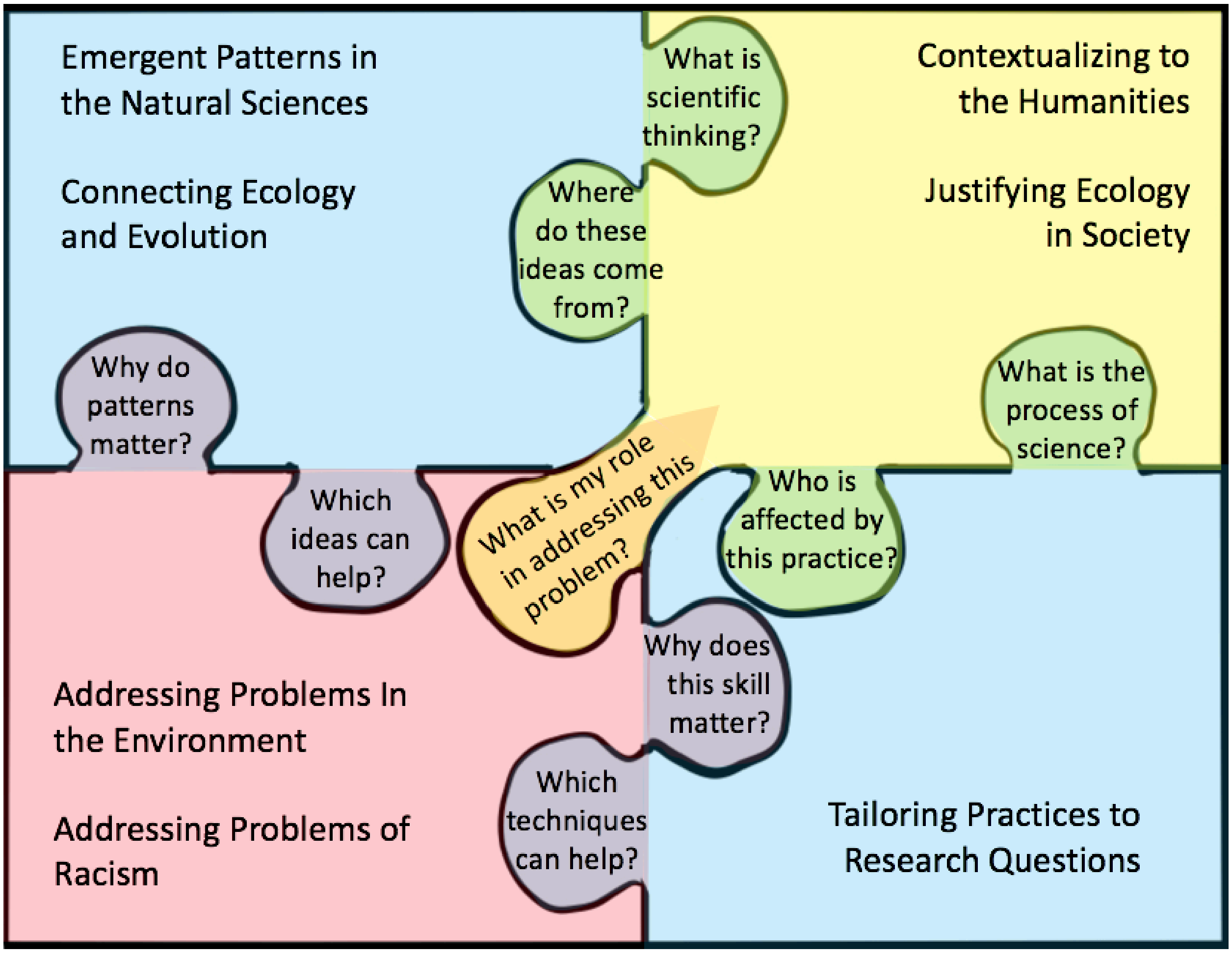

Figure 3: Opportunities presented by stacking high integration themes in lessons and assessments.

Each puzzle piece represents one theme or two themes with similar pedagogical benefits and limitations. Intrusions into a puzzle piece contain questions that illustrate a limitation of that piece's theme(s) which can be addressed by another theme from the extruding piece.

Themes rooted in Contextualization like *Contextualizing in the Humanities* and *Justifying Ecology in Society* can be used to generate assessments and lessons in which students are motivated to learn ecology and understand where it comes from. However, these themes do not necessarily prepare students to actually do scientific work. This limitation can be ameliorated by pairing course materials that provide context with lessons on ecological research methods, such as those facilitated by the *Tailoring Practices to Research Questions* theme. An obvious choice of venue for this pairing is laboratory courses, though instructors may alternatively incorporate methodological content through the use of personal stories told by scientists (Carmel 2011; Story Collider Inc) or data-rich case studies about the environmental aspects of everyday life (Wyner and DeSalle 2020).

Our two problem-centered themes, *Addressing Problems in the Environment* and *Addressing Problems of Racism* could benefit from preceding course content in *Contextualizing in the Humanities* or perhaps *Justifying Ecology in Society* to explore why ecologists would or should be called upon to solve problems in the first place. Students can use cultural and historical perspective to shape how they define their own responsibilities and limits as problem solvers. Further, students who are addressing problems can benefit from lessons in *Tailoring Practices to Research Questions*, so that they can use evidence to explain why they address problems in particular ways.

The proposal that instructors use different interdisciplinary strategies to build on one another in an integrated 4DEE lesson is supported by Prevost et al.'s (2019) early examples of 4DEE lessons. In this publication, the authors describe two lessons that each spanned multiple classes, in which students covered content from each of the four dimensions by moving fluidly from conceptualizing activities (such as identifying patterns in data) and contextualizing activities (such as identifying social drivers and impacts of species decline) before investigating potential problem-solving efforts.

Limitations and Future Research

In this study, we collected blank assessments only. Our interpretation of these assessments does not include the context of lectures or other course materials, so we do not claim that our interpretation represents these courses in their entirety. We also do not know how students responded to assessment questions. As with previous surveyors of course assessments (Laverty et al. 2016), our interpretation is only of the *potential* these assessments created for student learning, not of what they actually learned. Our study documents also represent only a small fraction of ecology assessments, a sample which is biased by our selection of only English-language courses and our solicitation of surveys in listservs frequented by instructors in the United States.

Future researchers can continue to develop our understanding of ecology assessments by examining students' responses to questions in each of the seven themes we have identified. In particular, researchers could study whether student performance on questions in these themes indicates accomplishment of specific learning goals, such as understanding common pedagogical principles of ecology (Knapp and D'Avanzo 2010). Further, future researchers may wish to study the benefits and barriers instructors face when using these themes while writing and grading assessments.

Conclusions

The elements of the 4DEE framework are well-represented in existing ecology-content courses. Co-occurrence of elements in different dimensions is common in ecology assessments. High integration assessment questions tend to fall into a few specific categories: *Addressing Problems in the Environment*, *Addressing Problems of Racism*, *Emergent Patterns in the Natural Sciences*, *Tailoring Practices to Research Questions*, *Contextualizing in the Humanities*, *Justifying Ecology in Society*, and *Connecting Ecology and Evolution*. These themes may provide a useful guide for instructors looking to use the 4DEE framework to deepen their students' understanding of ecology. In particular, lessons that combine approaches in different high-integration categories may help students understand the human context of ecology, the scientific patterns within it, and the limited but important potential that ecology has to address problems.

Appendix A- Survey

Integration Across Dimensions in Ecology Assessments

Are you a current or previous instructor of a college or university course that teaches ecology content in the English language?

- Yes
- No
- Not sure

Do I have your permission to quote or include pictures of your course materials in publications that are produced from this research? If I do not have your permission, I will still include your course materials in data analysis, but I won't directly quote your course materials in publication.

- No, please keep my course materials private (this is the default if you do not answer this question)
- Yes. Please credit me.
- Yes, but please keep me anonymous

What course are you submitting materials for? (if you are able to submit materials for multiple courses, please do so on separate surveys)

- Introduction to Biology
- Ecology
- Evolutionary Biology
- Animal Behavior
- Genetics
- Environmental Science
- Other (please specify)

What is the name of the college or university for which you teach this course?

What department is the course offered through?

- Biology
- Environmental Science
- Other (please specify)

How many students are typically in one section of the course?

This course (select all that apply):

- Fulfills a course requirement for non-majors
- Is an elective for non-majors

- Is an introductory course for majors
- Is an upper-level required course for majors
- Is an elective for majors
- Other: please describe

The students in your class are primarily (select all that apply):

- First years/ Freshmen
- Sophomores
- Juniors
- Seniors
- Graduate Students
- Other: please describe

Who grades your course assessments? (select all that apply)

- The instructor of record
- Graduate Teaching Assistant(s): If so, how many?
- Undergraduate Teaching Assistant(s): if so, how many
- Other: please describe

Where do you get your assessment questions or prompts? Please select all that apply:

- I, the instructor of record, write them
- Other instructors in the department write them

- Teaching Assistants write them
- I use questions from a question bank
- Other: please describe

Would you describe this course using any of the following terms? Please select all that apply:

- Focused on a single discipline
- Cross-disciplinary
- Multidisciplinary
- Interdisciplinary
- Other: please

In which years have you taught this course? Please select all that apply:

- 2020
- 2019
- 2018
- 2017
- 2016
- 2015
- 2014
- 2013
- 2012
- 2011

- 2010
- 2009
- 2008
- 2007
- 2006
- 2005
- 2004
- 2003
- 2002
- 2001
- 2000
- Before 2000

Rate your familiarity with the 4DEE (Four Dimensional Ecology Education) framework.

- I have never heard the term "4DEE"
- I have heard the term "4DEE" but don't know what it means.
- I know the term but haven't aligned my teaching to it
- I have aligned some of my teaching to the 4DEE framework
- I have aligned all of my teaching (when possible) to the 4DEE framework

How many years have you taught (any) courses at the college or university level?

What is your title?

- Lecturer
- Senior Lecturer
- Professor of Pedagogy
- Instructor
- Adjunct Faculty
- Visiting Professor
- Professor
- Associate Professor
- Assistant Professor
- Other, please specify

Is your institution classified as one of any of the following?

- Historically Black Colleges and Universities
- Hispanic-Serving Institutions
- Tribal Colleges or Universities
- Native American Non-Tribal Institutions
- Minority Serving Institutions
- Alaskan Native- or Native Hawaiian-Serving Institutions
- Asian American- and Native American Pacific Islander-Serving Institutions
- Predominantly Black Institutions
- I don't know
- Other, please specify:

Is your institution classified as a(n):

- R1 University
- R2 University
- Liberal Arts College
- Community College
- Other, please specify:

What is your name?

May I contact you for future, related research projects?

Yes

No

(If Yes)

What is your email address?

Please upload course documents in the following items. If you do not have the document specified, that's fine. Anything you can contribute will be valued. If you’re not sure where to upload a document, use any of the following items. Please do not upload examples of student work.

Upload course syllabus here

Upload final or midterm exam here. Please include answer key if possible.

(Only one file can be uploaded in this space. Please upload multiple files in zip folder or in additional upload spaces, below.)

Upload other summative assessments (essay prompts, project assignments, lab report assignments, etc.) here. Please include any rubrics or other scoring criteria you have available. (Only one file can be uploaded in this space. Please upload multiple files in zip folder or in additional upload spaces, below.)

Upload any other assessments you're willing to share (including formative assessments such as quizzes or writing assignments) here. (Only one file can be uploaded in this space. Please upload multiple files in zip folder or in additional upload spaces, below.)

Additional Upload Space

Additional Upload Space

Additional Upload Space

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Additional Upload Space

Appendix B- Examples of No Integration and Low Integration Questions

No Integration

Ecology Concepts

Explain why production efficiency is much higher in insects and amphibians than in mammals and birds. (An idea considered during the caterpillar lab.)

Survey respondent requested that their course materials be shared anonymously

This question comes from an exam in an Ecology course. This question was coded for the Ecology Concepts element productivity. Though this question asks students to explain why an ecological phenomenon is happening, it is not a high integration question because it does not include elements from another dimension.

Ecology Practices

If an ecologist is studying the correlation between two variables and measures their correlation coefficient (r) to be 0.97, this indicates

a. extremely strong negative correlation between the two variables.

b. extremely strong positive correlation between the two variables.

c. relatively weak positive correlation between the two variables.

d. essentially no correlation between the two variables.

Survey respondent requested that their course materials be shared anonymously

This question comes from an exam in an Ecology course. This question was coded for the Ecology Practices element statistics.

Human-Environment Interactions

Why is there reason to be concerned that human activities will cause a mass extinction event?

a. Because human activities are causing more extreme environmental changes than have been observed in the rock record.

b. Because human activities are causing environmental changes at a rate that is faster than has been observed in the rock record

c. Because more species are now going extinct than have ever gone extinct in the past.

d. Because in the past, organisms have not shown the ability to adapt to changes in their environment.

Ashley Bales, Pratt Institute

This question comes from an exam in an Ecology course. It was coded for the Human-Environment Interactions element human accelerated change.

human accelerated change

Cross-cutting Themes

What are the four evolutionary processes?

Which of the above processes can:

a. Lead to adaptation

b. Increase genetic variation within a population

c. Reduce the probability that speciation will occur

Survey respondent requested that their course materials be shared anonymously

This question came from an exam in an Ecology course and it was coded for the Cross-cutting Theme element evolution.

Low Integration

Ecology Concepts and Ecology Practices

Draw a climate diagram representative of the conditions in the Grassland ecosystem you are studying (I don't expect you to know absolute numbers for your y-axes but do your best to speculate on potentially reasonable values based on info provided). Your location has mean annual precip = 100 mm, mean annual temperature = 5.5C, elevation = 700 m), Hints: Be sure to label your axes and match up appropriate values and identify the growing season by circling and do your best to follow proper diagram guidelines. You can use symbols in place of colors for your lines. No figure caption required!

Anne McIntosh, University of Alberta

This question came from an exam in an Ecology course. It was coded for the Ecology Concepts element biome type and the Ecology Practices element data skills.

Ecology Concepts and Human-Environment Interactions

The overexploitation of cod in the North Atlantic releases crab and shrimp from predation pressure and results in a boom in the number of crab and shrimp. The increased number of crab and shrimp cause a decline in zooplankton abundance, which subsequently causes an increase in phytoplankton abundance. This change in the food web is an example of which of these?

(A) Top-down control

(B) Bottom-up control

(C) Behavioral cascade

(D) High resilience

Survey respondent requested that their course materials be shared anonymously

This question comes from an exam in an Ecology course. It was coded for the Ecology concepts elements regulators, trophic cascades; stability, disturbance; competition, mutualism, predation; food chain, food web; and behavior. It was coded for the Human-Environment Interactions element agricultural ecosystems (a category which includes fishing). This question is a good example of our methodology in that questions were coded for all elements that came up in a question, even if the element occurred in a wrong answer (e.g., “Behavioral cascade”).

Ecology Concepts and Cross-cutting Themes

If an ecologist is measuring the primary production of an ecosystem, what is being measured?

a. the number of autotrophs

b. species richness

c. biomass

d. chemical energy

Survey respondent requested that their course materials be shared anonymously

This question came from an exam in an Ecology course. It was coded for the Ecology Concepts elements biodiversity and productivity and the Cross-cutting Themes element pathways of matter and energy.

Ecology Practices and Human-Environment Interactions

Find a "Linnaeus" species with the specific epithet "officinale/is", first described in the 1735 publication of Systema Naturae. Linnaeus used this specific epithet for plants of known medical benefit, because the "officina" near a medicinal garden was where extracts and tinctures were produced. What is the scientific and common name?

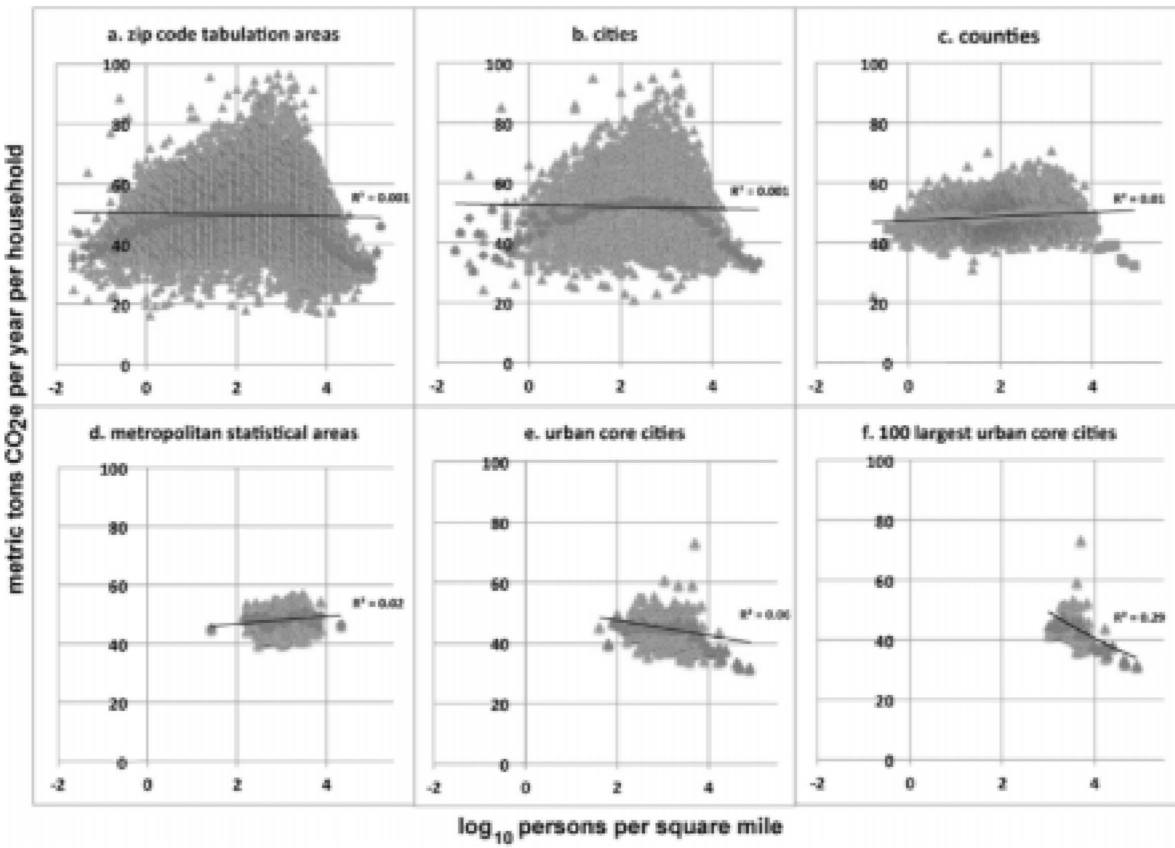
Garden section: A / B / C / D / E /F

Look online to briefly describe its medicinal properties:

Survey respondent requested that their course materials be shared anonymously

This question came from a worksheet completed during an Ecology lab. It was coded for the Ecology Practices elements species identification and collaboration (because students were instructed to work in pairs) and the Human-Environment Interactions element ecosystem services.

Ecology Practices and Cross-cutting Themes



The above plot indicates:

a. no correlation between CO2 emissions and zip code

b. a strong negative correlation between CO2 emissions in the largest cities

c. no predictive relationship between population density by county and CO2 emissions

d. all of the above

e. a strong positive correlation between CO2 emissions and populations density

Ashley Bales, Pratt Institute

This question came from an exam in an Ecology course. It was coded for the Ecology Practices elements statistics and arguing from evidence. It was coded for the Cross-cutting themes element stability and change. It was also coded for the Human-Environment Interactions element climate change.

Human-Environment Interactions and Cross-cutting Themes

All else being equal, which of the following species would you expect to be most able to evolve and keep pace with climate change?

(A) A species that reproduces twice a year, and is part of a large, genetically diverse population

(B) A species that reproduces once every two years, and is part of a large, genetically diverse population

(C) A species that reproduces twice a year, and is part of a small population with moderate genetic diversity

(D) A species that reproduces once every two years, and is part of a small population with moderate genetic diversity

Survey respondent requested that their course materials be shared anonymously

This question came from an exam in an Ecology course. It was coded for the Human-Environment Interactions element climate change and the Cross-cutting Themes element evolution. It was also coded for the Ecology concepts elements life history and global climate change.

Appendix C- Frequency of Element Codings

The appendix presents the number of times elements of each 4DEE dimension coded in this study. The sum of the contextual units that were assigned codes in each dimension is displayed to the right of the dimension name. Note that the length, content, and assessment type of a contextual unit varies greatly between study documents, so quantitative comparisons between elements are thus unlikely to yield meaningful data.

	Element (code)	Number of times found in questions
Ecology Concepts		879
	ecology in this course	22
	biosphere	2
	global climate change	31
	global biogeography	21
	biome	4
	latitude and elevation	13
	biome type	55
	landscape	7

	watersheds	1
	patches, corridors, barriers	20
	gradients	7
	ecosystem	10
	trophic levels	24
	regulators, trophic cascades	15
	productivity	42
	predation, carnivores, herbivores	18
	nutrient cycles	61
	food chain, food web	27
	community	7
	succession	17
	stability, disturbance	18
	habitat type	14
	competition, mutualism, predation	61
	biodiversity	51
	behavior	18
	population	12
	life history	56
	growth curves	54
	organisms	7
	resources and regulators	70
	habitat and niche	65
	(a)biotic features	49

Ecology Practices		547
	communicating and applying ecology	56
	natural history	36
	collaboration	60
	investigations	3
	experimental design	77
	evaluating claims with evidence	72
	arguing from evidence	106
	fieldwork	12
	species ID	12
	habitat assessment	0
	GIS	4
	quantitative reasoning	3
	statistics	42
	spreadsheets and R	10
	modeling and simulation	18
	informatics	0
	data skills	36
Human-Environment Interactions		207
	ecosystem services	20
	ethics	13
	environmental philosophies	8
	environmental justice	3

ecological economics	6
"sustainability"	3
human-accelerated change	29
toxicology	4
climate change	49
resource management	24
stewardship	5
engineering	0
conservation biology	15
agricultural ecosystems	28

Cross-cutting Themes 481

spatial and temporal	0
stability and change	23
scales	12
evolution	103
biogeography	48
systems	91
structure function	68
pathways of matter and energy	136

Appendix D- 4DEE Elements Codebook

This codebook contains the names and working definitions for the codes used in my first coding cycle, in which I coded for the presence of 4DEE framework elements. This table is organized by dimension and groups sub-codes under their parent codes.

Dimension

Ecology

Concepts

Codes	**Sub-codes**	**Description**	**Origin**
a priori categories determined by the 4DEE framework		*When is code applied?* *When is it specifically not applied?*	*codes are determined a priori by 4DEE, but sometimes other sources influence code definition and application.*
Biosphere		questions that explicitly ask students about living organisms at the "biosphere" or "global" level, excluding questions about global climate change or global biogeography.	
	global climate change	Questions that ask about climate change, global warming, or carbon emissions, only when discussed at the global level. Questions that ask about, say, carbon emissions on Earth in general (without specifying a region) can be assumed to be global.	
	global biogeography	Questions about where one or multiple species is distributed at a global level, not specified to a region of the earth. May include questions about the general locations of different biomes across the plant (e.g., tropical forests at equator),	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)

		continental drift and previous continent configurations (e.g., Pangea)	
Biome		Questions in this general bin should be about biomes (likely using the word "biome" either in question or in the answer), not about latitude, elevation, or a specific biome type.	
	latitude and elevation	Questions about the role that latitude and elevation play on species distributions in a given biomes. Might include latitudinal gradients of species richness (i.e., about how there are more species near the equator), or the general idea that climate change drives species to different elevations/latitudes	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
	biome type	Questions about a specific type of biome or comparing multiple specific biomes. The biome should be named in the question or (potential) answer).	
Landscape		Questions that are about the landscape ecology. Landscape ecology is about the arrangement of different types of habitat in a space (e.g., the layout of where forests, plains, and lakes are in a national park). May include questions about landscape heterogeneity or mosaics. Doesn’t include questions that are specifically about watersheds, gradients, or patches.	

	watersheds	A watershed is the area of land (something like the size of a city, though it varies a lot) that drains into a single stream. Questions coded for this will probably specifically mention "watershed" or prompt for it in the answer.	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
	gradients	Questions about one or multiple species that change along a gradient of some abiotic factor (elevation, latitude, soil moisture, sun exposure, etc.)	
	patches	Includes questions that specifically mention a patch of habitat, also includes questions about habitat corridors, edge effects, habitat buffers, and habitat fragmentation into patches. Doesn't include questions about island biogeography.	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
Ecosystem		Questions about ecosystem ecology that don't fit into the categories below. Questions will probably mention the term "ecosystem."	
	trophic cascades	Questions about trophic cascades. Trophic cascades happen when a change in the abundance of carnivores causes an indirect change in the abundance of plants (or other primary producers), because the carnivores eat the herbivores that eat the plants.	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
	nutrient cycles	Questions that include any mention of a nutrient that changes from one form to another (i.e. organism to soil) or a specific mention of a nutrient being at one point in its cycle (e.g., soil is one location in the nitrogen cycle).	

		Doesn't include questions about a nutrient that's just in one species (without mention of the cycle) (e.g., a question about how a flower need potassium).	
	productivity	Questions that cover the topic of net and gross primary productivity, including assimilation efficiency, production efficiency, etc.	
	food chain	Questions that ask students anything about a food chain or web, or questions that don't mention these by name but are discussing at least three species in a chain or web where some consume the others (e.g. foxes eat rabbits eat clover)	
	predation broadly	At this ecosystem level, predation refers to the general idea of predators / carnivores in a food web, generally referring to multiple species and/or across multiple tropic levels.	
	trophic levels	Questions about the flow of energy through an ecosystem through the consumption of producers by consumers. Question may include a trophic pyramid. Question may be about one or multiple trophic levels (but if only one, should probably mention "trophic" or something about the amount of energy species at that level gain from their food).	

Community		Questions about assemblages of multiple species that cannot be placed in one of the more specific categories below. Probably mentions "community" specifically. This category does not include broader ecological levels (i.e. though an ecosystem contains multiple species, a question about a whole ecosystem doesn't count in this category).	
	behavior	Questions about behavior between species, not including behavior among individuals of a single species (e.g. sexual selection, intraspecific competition). More focused on HOW an animal does predation, competition, mutualism, hiding, or learning/communicating across species (as opposed to, say, measuring the amount of predation. that goes in the predation code).	
	succession	Questions about the change in the distribution and abundance of different species over relatively short time scales (weeks to maybe 100 years, often). I.e. the species are changing due to succession, not evolution or change in abiotic factors of the environment (seasons, environmental destruction, etc.) Often about plants, though not exclusively.	

	stability	Questions about change or lack of change in a community over time, in terms of which species are present in the community and how abundant they are (not due to regular patterns like seasons or day/night). Can include questions about climate change if the change involves multiple species. Can include questions about the community's response to disturbance (development, natural disasters).	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
	competition, mutualism, predation	Only questions that include these concepts as an interaction between two or more species (i.e. not intraspecific competition). May include the lotka-volterra models phase planes, etc.	
	biodiversity	Questions that ask about biodiversity or species richness, i.e. nearly any question that asks about the number of species present in a given space and the number of individuals among species. Includes alpha, beta, gamma diversity, though the question doesn't need to be this specific.	
	habitat type	Questions about life for multiple species in a given habitat (e.g. terrestrial, aquatic, marine, wetland, soil, etc.) Can be on a smaller scale than questions about biomes.	
Population		Questions about populations that don't fall into either the life history or growth curve category. Should generally be questions about one (or multiple) populations of a species, not the whole species itself.	

	life history	Questions about life history of a given species including: life cycles, r/k selection, phenotypic plasticity, morphs, metamorphosis, Grime's triangle, energy budget questions about metabolism and clutch size and lifespan vs reproduction tradeoffs, age at maturity and senescence	Cain ML, Bowman WD, Hacker SD. 2008. Ecology. Sinauer Associates, Inc. (Textbook)
	growth curves	Questions about exponential and logistic growth curves (sometimes called J and S curves), including those about carrying capacity, the general concept of density dependence	
Organisms		Questions about one species of organism that don't fall into one of the more specific categories below.	
	habitat and niche	Questions that specifically mention the habitat or niche an animal lives within. Can be fundamental or realized niche.	
	resources and regulators	Questions about the abiotic and biotic factors what either increase or decrease the abundance of a species. Doesn't include questions that more specifically address another topic in a different code. Does include questions about climate change if only one species is involved (including interactions between one species and an abiotic factor).	
	a/biotic	Questions that describes aspects of the environment a species can live in, typically needs	

		to include either the word "biotic" or "abiotic" in the question or potential answer.	
Dimension Ecology Practices			
Science Communication		Assessment components that ask students to do or reflect on science writing, presentation, or other forms of communication. Must include either a defined genre (e.g. lab report, infographic, etc.) or a defined audience (e.g. a young child, conference attendees). Includes application and extension programs. Also includes policy work.	
Collaboration		An assessment component that asks students to either do or reflect on collaboration. Includes any group assignment or specific instructions for working with another person or pooling data collected by multiple people. Includes questions that ask students to reflect on their experiences working with another person or to reflect on a collaboration they were not a part of (e.g. a question about how two scientists shared responsibilities in a study).	
Experiments		Includes assessment components where students are doing an experiment, even if they're not asked specifically to comment on (or develop) the experimental design. Does not include questions that just references any experiment that exists.	

	Arguing from Evidence	Questions in which a claim is generated by the student and students must provide some sort of evidence for it. Evidence must have a source e.g. a data table or figure or explicitly referenced study, not just a statement (e.g. a multiple choice question where a student selects something like "yes because ants live underground" would not count). Also includes questions in which students predict what additional evidence they would need to support a related argument (that they have come up with).	
	Evaluating Claims w/ Evidence	Questions in which a claim is provided to the student and they assess what it means and whether evidence supports it. Evidence means some sort of source e.g. a data table or figure, not just a statement. Also includes questions that ask students what evidence one would need to make a particular argument.	
	Experimental Design	Questions that ask students to create or evaluate any component of creating an experimental design (e.g. generate a hypothesis) or question about how experiments work (e.g. a question that asks why there are replicates in a study). Includes questions that ask students to explain a particular method or technique for getting a type of information (e.g. a question that asks how researchers measure rate of consumption).	

Quantitative Reasoning		Questions that ask students to do math, use equations to answer questions, or make other judgements about percentages, units, or models. Does not include questions from subcategories below.	
	Informatics	Questions that ask students to do or reflect on the analysis, collection, and management of large data sets.	
	Modeling and Simulation	Questions in which students are creating some sort of model or simulation (or a component of one). The model can be mathematical, graphical, computational, symbolic, or pictoral (e.g. this includes concept maps and drawings of interaction webs) Does not include questions that simply mention an existing model and ask students to analyze it or manipulate it (e.g. does not include students putting different values in an online interface simulator).	
	Spreadsheets and R	Questions that ask students to make (or reflect on the nature of) a spreadsheet on a computer. Includes data analysis in R or Excel (including calculation of summary statistics, though that would also be coded with statistics, below). Does not include questions in which students are asked to write down data in an analog table.	

	Data Wrangling and Viz	Data wrangling questions ask students to organize existing data (almost definitely on a computer), perhaps doing actions like changing between long and wide data, filtering and sorting data, or something similar. Data visualizations ask students to create a graph or other representation (including diagrams or even an artistic representation) of a pool of data. This code category does not include questions that ask students to draw a graph without referencing specific data (e.g. a question that asks students to draw an exponential growth curve). This code also doesn't include questions in which students are simply asked to collect data.	
	Statistics	Questions that ask students to do or reflect on statistical tests, including the calculation of summary statistics and questions about the application of a statistical test (e.g. a question that asks if a t-test would be a good fit for a certain study)	
Fieldwork		Activities in which students go into the field (will likely be outdoors, though could be indoors if they are discussing an indoor space as an ecological site). Does not include activities and questions that would better fit under the following sub categories.	

	GIS	Activities and questions in which students use or discuss GPS coordinates, plotting on a GIS program in the field, or creating/manipulating/analyzing GIS maps on a computer. Also includes remote sensing.	
	Species ID	Identifying specimens to some taxonomical level (or morphospecies) in the field or lab or even classroom. Includes questions that describe a species' traits and ask students to ID from that description (or vice versa).Also includes specimen preservation.	
	Habitat Assessment	Questions or activities about the formal process of habitat assessment, which may include stream and bank structure analysis, species ID, soil moisture assessment, or other ecological factors relevant to the area.	
Natural History		Questions or activities in which students give a species account or describe an environment, including details about what the species eats, aspects of its structure, and where it lives. Students' responses may come from observation in the field.	
Dimension			
Human-Environment Interactions			

ethics		Questions in which students respond to an ethical situation that is not encompassed in the following subcategories	
	ecological economics	Questions that ask students about philosophies and practices of economics related to ecological principles. May include questions about the Jevons Paradox or the monetary value of ecosystem services.	
	environmental justice	Questions that ask students about activism, advocacy, policy, or issues at the intersection between environmental hazards and social systems of oppression. Will likely include questions about environmental racism and/or stratification of environmental impacts by socioeconomic class. May includes issues at the local or global level. Does not include questions about environmental hazards alone, without considering social factors such as (typically) racism or classism.	Environmental Justice Explainer StateImpact PA https://stateimpact.npr.org/pennsylvania/tag/environmental-justice/
	social construction of sustainability	Questions about the philosophy and interpretation of "sustainability," such as questions about Shifting Baseline Syndrome, cultural themes inherent to sustainability practices, or social construction of what it means to be sustainable. Questions may engage with any/all of the three pillars of sustainability: ecological, economic, and social). Generally concerned with perspectives on what humans do with natural	Purvis, B., Mao, Y. & Robinson, D. Three pillars of sustainability: in search of conceptual origins. Sustain Sci 14, 681–695 (2019). https://doi.org/10.1007/s11625-018-0627-5

		resources. Does not include questions that superficially discuss sustainability practices without engaging with the nature of the practice and/or term "sustainable."	
	environmental philosophies	Questions that ask students to reflect on or identify specific environmental philosophies, including: Indigenous Sciences, Traditional Ecological Knowledge, anthropocentrism, biocentrism, etc.	Simpson, Leanne. "Indigenous environmental education for cultural survival." Canadian Journal of Environmental Education (CJEE) 7.1 (2002): 13-25. Bang, Megan, Ananda Marin, and Douglas Medin. "If indigenous peoples stand with the sciences, will scientists stand with us?." Daedalus 147.2 (2018): 148-159. Wanting, Xu. Encyclopedia of Education for sustainable

			development "Environmental Philosophy" Oct 2018. http://www.encyclopediaesd.com/blog-1/2018/10/19/environmental-philosophy
resource management		Questions about resources that aren't represented in the following subcategories	
	stewardship	Questions that ask students about environmental protection and improvement by way of cultural, systemic, or lifestyle changes at the individual, community, or institutional level.	
	conservation biology	Questions that ask students about research and policy done by government organizations and other large institutions to understand threatened species and install technology, policy, or other mechanisms to reduce environmental harm.	
	engineering	Questions that ask about biomimicry, the ecology of gene drive systems, or other engineering practices influenced by ecological principles.	
	agriculture, fisheries, forestry	Questions that ask about or include discussion of agriculture, fisheries, and forest management, includes questions about herding, ranching, or gardening(unless specified as non-commercial e.g. backyard flower gardening)	

human-accelerated change		Questions that ask about the effects humans have on the environment that do not include the subcategories listed below. Include questions that confront erroneous ideas about "pristine" ecosystems or systems in complete equilibrium. Generally concerned with what humans do with nature itself (not necessarily the resources nature provides). Does not include questions about natural disasters or diseases unless questions is specifically referencing the human causes behind that event.	
	toxicology	Questions about pollution, including those about biomagnification and bioconcentration	
	climate change	Questions about climate change, global warming, or greenhouse gases at any scale.	
Ecosystem Services		Questions about ecosystem services. May include pollination, pest control, pollutant filtration; production of food, energy, and other resources; and cultural resources used in spiritual, recreational, educational, and other cultural practices.	
Dimension Cross-cutting Themes			
SpaceTime			
	Evolution	Questions about evolution, including those about population genetics, inheritance, fitness, epigenetics, speciation, and phylogenetic trees.	Brownell, Sara E., et al. "BioCore Guide: a tool for interpreting the core concepts of

		Doesn't include questions that simply mention a mutation.	Vision and Change for biology majors." *CBE—Life Sciences Education* 13.2 (2014): 200-211.
	Biogeography	Questions about a species' range and native, exotic, and invasive species.	
	Stability and Change	Questions that ask students to reflect specifically on stability or change in a given system, or that ask students to compare/contrast two time points or locations. Like to use the terms "stability" or "change" explicitly. Does not include questions that only superficially address stability and/or change (e.g. nearly any graph axis).	
	Scales	Questions that are about the significance of a specific scale or that ask students to compare something across multiple scales.	
Systems		Questions about a range of topics that consider how collections of cellular, anatomical, or ecological components work together to produce some sort of function, typically related to responding to change in the environment. Includes topics such as population abundance and distribution, networks, and the role of biodiversity on ecosystem function. Could also include questions at the level of the individual organism that cover topics about acclimation,	Brownell, Sara E., et al. "BioCore Guide: a tool for interpreting the core concepts of Vision and Change for biology majors." CBE—Life Sciences Education 13.2 (2014): 200-211.

	feedback loops, homeostasis, chemical signaling, and development.	
Pathways	Questions about the transformation of matter and/or energy, including topics such as productivity, trophic levels, nutrient cycles, and biochemical pathways such as photosynthesis.	Brownell, Sara E., et al. "BioCore Guide: a tool for interpreting the core concepts of Vision and Change for biology majors." CBE—Life Sciences Education 13.2 (2014): 200-211.
Structure Function	Questions that ask students how physical and chemical characteristics relate to physiological or ecological function. May include questions about the role species' characteristics play in species interactions, the function of anatomical structures and their constraints, surface area to volume ratios, and even structures of molecules or cells. Does not include questions about structure or function alone, without in some way referencing the other.	Brownell, Sara E., et al. "BioCore Guide: a tool for interpreting the core concepts of Vision and Change for biology majors." CBE—Life Sciences Education 13.2 (2014): 200-211.

Conclusion

In completing the research presented in this dissertation, my overarching goals were first to understand how anthropogenic change in the environment influences bee social learning, and to next understand how ecology courses prepare students to make sense of these social and scientific issues.

In Chapter 1, I found that social cues influence bee foraging behavior on subsequent trips when the cue is no longer present, and that this influence is strongest for misleading social cues. This finding suggests that bumble bees may be more likely to learn the characteristics of the flowers they are visiting and retain that information for future trips when they are foraging with conflicting information, as a bee might in nature when observing social cues from other bee species with different foraging preferences.

In Chapter 2, I found that bees do not align their foraging with social cues after they have been exposed to a neonicotinoid pesticide. This finding may explain previous research that shows that groups of bees are less efficient at pollinating after pesticide exposure, even though pesticide exposure does not affect the pollination efficiency of individual bees foraging alone (Stanley et al. 2015). Pesticides may impair some emergent benefit of group foraging, such as the social cue communication between individuals that facilitates identification of rewarding flowers.

In Chapter 3, I found that nearly two-thirds of assessment questions used in Ecology courses asked students to integrate across dimensions of the 4DEE framework. Most often, the questions paired ecology concepts with concepts from other fields of the natural sciences or with quantitative concepts used in research practices. Questions that paired ecology concepts with human-environment interactions were less frequent and occurred less than half as often as either of the first two pairings. However, when instructors did ask students about humans and the environment, the questions tended to ask for thoughtful consideration of how concepts in different disciplines were connected. These human and environment connections were hallmarks of three of the seven themes I identified to categorize and describe high integration questions in ecology assessments. These themes had complimentary potential strengths and limitations for student learning. Future instructors can reference these themes to guide their integration across dimensions of the 4DEE framework.

The studies in this dissertation suggest several interesting areas for future research. Building on Chapters 1 and 2, further animal behavior research could discern how ephemeral social cues influence bee foraging over longer time spans than our overnight test and the ecological consequences for the lingering effects of social cues in the field. Specifically, Chapter 2 raises the possibility that decreased social cue use after neonicotinoid exposure is the mechanism by which groups of foragers pollinate less efficiently than unexposed groups do. To explore this, future work would need to scale up from individual-level to group-level foraging. In particular, future researchers could explore this by evaluating how bees in the lab respond to dynamic social cues, such as the response of a naïve group of foragers to an experienced guide while multiple bees visit flowers simultaneously, and how these dynamics change with neonicotinoid exposure. Building on Chapter 3, future research could approach my study data with mixed methods, integrating the qualitative approach I took with additional quantitative analyses about the extent of 4DEE integration in various classes and contexts. Further, researchers could use this mixed-methods approach to evaluate the impact of integration across

4DEE dimensions on student learning, both in students' content mastery and in their motivation to understand ecological phenomena.

Viewed together, these studies ask similar questions from opposite perspectives. The first two chapters together ask how human choices influence ecosystems, the third how ecosystems are made meaningful to humans. In addressing this first question, Chapter 1 contributes insight into animal cognition with a bumble bee model. Bumble bees are valuable subjects for social information research because they perform complex cognitive tasks, like learning to efficiently identify and access foraging resources in a diverse and continuously changing field of flowers, with a tiny, seemingly simple neurological system (Leadbeater and Chittka 2007b). In Chapter 1, I add novel insight into how bees perform these complex cognitive tasks by showing evidence that bees learn more about floral resources when they are presented with information from a social cue that conflicts with their own experience. In Chapter 2, I elaborate this insight by investigating how bees' balance of social information and personal trial-and-error is complicated by pesticide exposure. While I expected to find that bees *increase* their use of social cues to compensate for cognitive losses caused by neonicotinoids, I instead found that exposed bees do not align their foraging with social cues, i.e. they instead use social cues less than unexposed bees do. This finding provides a potentially critical detail about bee foraging, that bees cannot or do not compensate for pesticide exposure using social cue shortcuts. In Chapter 3, I asked how bee declines—and many other ecological topics—are made meaningful to students in classrooms. I identified seven themes of highly integrated assessment questions that can be used by instructors who want to describe how they currently integrate ecology with other disciplinary concepts or who want to explore new ways of approaching integration. Further, this research sets a vital foundation for future evaluations of how integrated ecology teaching can improve. In particular, if ecological information is valuable in addressing real-world problems (such as bee decline), then improved ecology education should better prepare students to bring their ecology knowledge to problem-solving teams composed of people with diverse expertise, communicating across disciplines and perspectives to effect change.

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