

Is everything everywhere? A hands-on activity to engage undergraduates with key concepts in quantitative microbial biogeography

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ABSTRACT The ubiquity and ease with which microbial cells disperse over space is a key concept in microbiology, especially in microbial ecology. The phenomenon prompted Baas Becking's famous "everything is everywhere" statement that now acts as the null hypothesis in studies that test the dispersal limitation of microbial taxa. Despite covering the content in lectures, exam performance indicated that the concepts of dispersal and biogeography challenged undergraduate students in an upper-level Microbial Ecology course. Therefore, we iteratively designed a hands-on classroom activity to supplement the lecture content and reinforce fundamental microbial dispersal and biogeography concepts while also building quantitative reasoning and teamwork skills. In a class period soon after the lecture, the students formed three-to-five-person teams to engage in the activity, which included a hands-on dispersal simulation and worksheet to guide discussion. The simulation involved stepwise neutral immigration or emigration and then environmental selection on a random community of microbial taxa represented by craft poms. The students recorded the results at each step as microbial community data. A field guide was provided to identify the taxonomy based on the pom phenotype and a reference to each taxon's preferred environmental niches. The worksheet guided a reflection of student observations during the simulation. It also sharpened quantitative thinking by prompting the students to summarize and visualize their and other teams' microbial community data and then to compare the observed community distributions to the idealized expectation given only selection without dispersal. We found that the activity improved student performance on exam questions and general student satisfaction and comfort with the biogeography concepts. Activity instructions and a list of needed materials are included for instructors to reproduce for their classrooms.

KEYWORDS experiential learning, integrative learning, collaborative learning, active learning, reflective learning, microbiology, ecology, biogeography

We designed an active learning exercise for small student teams to explore and reinforce concepts in microbial biogeography and dispersal, which we had identified as challenging for students given past exam performance. We intentionally applied guidelines from experiential, integrative, collaborative, and reflective learning theories to do so. Experiential learning is the process of learning by direct experience, usually in the form of hands-on application of knowledge, and it has been found to be especially effective in biology education (1–4). Integrative learning theory aims to encompass multiple learning modalities and the interdisciplinary backgrounds of the students (5). This is crucial to successful collaborative learning, in which students work together within small teams and across the larger class community to synthesize and share their knowledge (6). Finally, we asked students to reflect on their experience

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with this active learning exercise and provide feedback for future implementations. These three approaches are fundamental to the social constructivist learning theory, which posits that students construct meaning based on their previous knowledge and experience (7). In social constructivism, instructor awareness, sensitivity, and adaptation to where the students “come from” is vital to identifying and correcting student misconceptions and misunderstandings (7, 8). Moreover, an instructor can leverage the insights of students from backgrounds different than their own to provide a new perspective or model of the learning topic (7, 8).

The activity presented here is a hands-on, team-based classroom exercise that takes approximately 80 minutes, with natural “pause points” for division into multiple class periods as necessary to accommodate meaningful discussions. The complete instructional materials for the team activity are available within this manuscript and its associated appendices, and are also available on FigShare (<https://doi.org/10.6084/m9.figshare.24243421.v1>). While the activity was modified on one occasion to be implemented virtually (see Possible Modifications), in our experience, it works best as an in-person experience.

In the course for which the activity was designed, students worked in diverse teams of 4–5, assigned non-randomly using the CATME Teammaker (9). Briefly, the teams were constructed to maximize the diversity of majors represented, minimize out-of-class scheduling conflicts for team projects, and harmonize across student-anticipated individual efforts. Students worked in their assigned teams on several projects and for in-class activities throughout the semester to encourage collaboration and integration of their understandings of the material. One of the first team activities was a community diversity exercise (“Counting the Uncountable,” see doi.org/10.6084/m9.figshare.24258727) that used craft pom microbial communities to ask teams to apply and calculate community diversity metrics and explore taxon abundance concepts in the context of a community (e.g., to identify rare and prevalent taxa). Each different color and size of pom (its phenotype) represented a different microbial taxon. Notably, here we use the term “taxon” to refer to an individual microbial population or species equivalent, as would be used in today’s microbiome research.

The biogeography activity presented here also used the craft pom communities as a model to actively reinforce concepts in microbial dispersal and environmental selection. But first, during a video lecture (flipped classroom), students were introduced to fundamental vocabulary and concepts, including the terms Biogeography, Endemic, Cosmopolitan, Neutral Model, Occupancy, Abundance, Deterministic, and Stochastic. The team activity described here started with a team worksheet that first prompted students to verify their prerequisite biogeography knowledge from the lectures, including the fundamental vocabulary and concepts.

Next, the worksheet provided activity instructions and data collection forms for a hands-on biodiversity simulation using the now-familiar craft poms (Fig. 1). Each team was given an environment card that listed different parameters to specify its pH and carbon, nitrogen, and water availability. The teams also received a guide that provided the niche preferences of each microbial taxon. Then, teams received a random collection of poms (several dozen), representing a subset of the full possible set of microbes (a.k.a. the metacommunity/regional species pool). Within their teams, the students first modeled how their randomly selected microbes would either die, survive, or thrive over one generation, given the precise parameters of their team’s environment and each taxon’s preferred niche. Dead microbes were returned to the instructor, but increases in the thriving populations happened only on paper using simple math. This step represented the environmental selection of fit microbes. Then, the fit community underwent a dispersal event (“Windstorm”) that resulted in the emigration of a random subset of their microbes to a neighboring team and the immigration of a random subset of microbes from a neighboring team into their pom community. This dispersal was performed by mixing or shaking the remaining poms in a container or bag, and then randomly scooping out a small portion (~25%–33%) to physically hand off to a

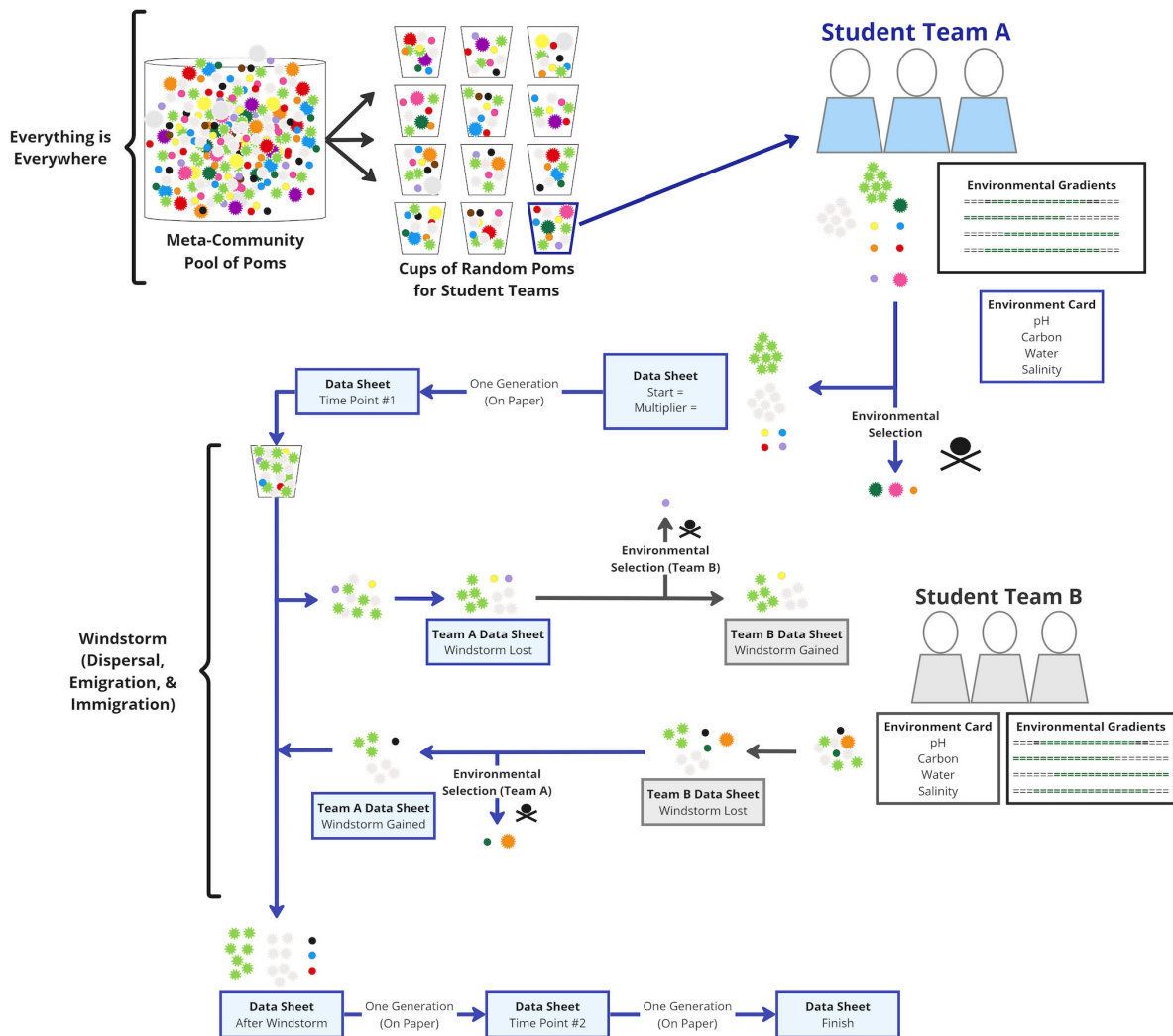


FIG 1 A flowchart of the biogeography activity.

neighboring team. We recognize that population growth is only represented on paper, so the poms undergoing dispersal are not a perfect reflection of the community composition. After the Windstorm-driven dispersal, the environmental selection process was repeated for two generations. To practice interpreting and visualizing data, the teams combined their collection of environmentally fit microbial community members with those of other teams to create a biogeographic distribution of microbial taxa across the possible environments (e.g., number of environmental cards/teams).

Finally, the worksheet guided the teams through data analysis and interpretation. First, teams categorized each taxon on an axis ranging from endemic to cosmopolitan, which requires an understanding of these terms and the variable that these terms describe (occupancy). They then used the abundance data to predict where specific taxa would fall on an abundance-occupancy graph and to interpret whether each conformed to the expectation of the neutral model. Finally, teams qualified their confidence in their projections based on their perceived observational effort of the community and taxa (e.g., sampling depth or coverage). They thus were asked to estimate their certainty in a taxon's perceived abundance (Are rare taxa really cosmopolitan/endemic, or just rare? How do we know? What more information is needed, if any, and why?). These follow-up questions were discussed among the whole class to encourage teams to collaborate, to compare their responses, and to elaborate on differing answers to ensure

students understand the spectrum of possible correct answers (where applicable) and the key distinctions underlying a correct answer vs an incorrect one. The worksheets were not graded, but the class discussions provided students feedback on their answers, and an instructor-developed worksheet key was provided to students to support exam preparation.

Intended audience and prerequisite student knowledge

This activity is intended for predominately upper-level (third- and fourth-year) undergraduate college students and first-year graduate students in fields related to biology, microbiology, ecology, or environmental sciences such as crop and soil sciences, geosciences, environmental engineering, and food safety and toxicology. Before this activity, students were introduced to fundamentals of microbial community ecology, including how to measure diversity, richness, evenness, rarefaction, rarity, and what an operational taxonomic unit (OTU)/taxon could represent. This team activity also assumes that students will have been given a lecture or other instructional materials on the basics of biogeography (our recorded video lessons are available here: doi.org/10.6084/m9.figshare.24243370) such that they can define microbial biogeography, the neutral model, occupancy vs abundance, stochastic vs deterministic, and endemic vs cosmopolitan.

Course delivery and learning time

The activity will take approximately 80 minutes to complete after the lecture material. Still, the exact duration depends on the size of the class and the number of teams included (we propose a maximum of 15 teams), with more teams requiring more time for inclusive discussion. However, it has natural break points that enable it to be pursued over multiple class periods and meet the instructor's timing needs. It could be extended with thorough discussion to cover a longer period, for example, a laboratory class period. We have also offered the activity virtually. Please see the Possible Modifications section.

Learning objectives

Upon completion of the associated lecture and this activity, students will be able to:

1. Define the following terms: biogeography, species-area relationships, neutral models, cosmopolitan, and endemic
2. Relate spatial observational effort to patterns of microbial diversity
3. Hypothesize how microbial diversity may change across environmental gradients and provide examples
4. Use models of abundance occupancy to identify taxa that fit the neutral expectation and those that do not
5. Explain how the environmental heterogeneity contributes to patterns of microbial populations and communities over space

This activity complements the associated lecture(s) by giving students an engaging, hands-on application of the biogeography concepts, and the worksheet explicitly connects the activity back to the lecture terms and concepts.

PROCEDURE

Materials

For each *class* of up to 75 students, working in teams of 3–5 students (min 10 teams, max 15 teams), the instructor and students will need the following materials:

1. A mixed pompom pool (composition and taxonomy detailed in the “field guide” Fig. 2; Table 1)
 - a. Assorted small (~1 cm) craft pompoms or comparable (~10 unique phenotypes) (Amazon, need one unit)
 - b. Small (~1 cm) sparkly craft green (or other unique color/size) pompoms or comparable (Amazon, need one unit)
 - c. Small (~1 cm) sparkly white craft (or other unique color/size) pompoms or comparable (Amazon, need one unit)
 - d. Assorted large (~4.5 cm) sparkly pompoms or comparable (~8 unique phenotypes) (Amazon, need one unit)
2. One large bowl or bag for mixing the pompom pool (this could be done ahead of time, but mixing the pool in front of students reinforces the randomness of their samples).
3. Up to 15 containers, cups, or bowls for distributing pompoms to teams (Amazon; need one container per team + some extras)
4. One printed copy of the Activity Environment Cards A–O, with the cards cut out (Appendix 1; need one copy of each card)
5. 22–32 Printed copies of Activity Instructions (Appendix 2; need two copies per team + two or more extras)
6. 12–17 Printed copies of Activity Data Sheet (Appendix 3; need one copy per team + two or more extras)
7. 22–32 Printed copies of Worksheet (Appendix 4; need two copies per team + two or more extras)
8. Classroom or student-supplied laptops, smartphones, or tablets for entering and sharing class data (at least one per team)
9. Up to 30 pens/pencils (at least two per team)
10. One pom “field guide” such as the one in Fig. 2 can be helpful for students during the simulation. We used an overhead projector to display the field guide to the class.
11. One collaborative spreadsheet for data entry (e.g., Google Sheets or OneDrive), such as this one: <https://tinyurl.com/368atmaw>
 These data could also be entered onto a paper form by students and then projected as an overhead to share with the class, but this would take more time because the worksheet would have to be passed around to each team rather than enabling co-working on a digital data form.

Of the above materials, each *team* of students will need the following:

- two copies of Activity Instructions (Appendix 2)
- one copy of the Activity Data Sheet (Appendix 3)
- two copies of the Biogeography Worksheet (Appendix 4)
- one container of mixed pompoms (may be slightly less than full for 15 teams; try to distribute the pompom pool as evenly as possible)
- one + computer or laptop for data entry if using digital data form
- one + pen/pencil

Faculty and student instructions

Instructors should provide the prerequisite lecture(s) either in the preceding class session or as a recording assigned before the activity, informing students that the following class session will be an activity. Before the activity day, instructors should obtain the pompoms and containers, then compose the pompom community pool as prescribed in Table 1. Instructors should also prepare the necessary copies of the Activity Instructions (Appendix 2), Activity Data Sheet (Appendix 3), and Worksheet (Appendix 4) as well as print one copy of the Activity Environment Cards (Appendix 1) and cut out the cards.



FIG 2 A "field guide" to the pompoms used in the biogeography activity. Numbers and descriptions correspond to the OTU number and description used in the activity sheets.

Finally, instructors should prepare a collaborative data form/spreadsheet for teams to combine the data generated during the activity. It should look like an empty copy of the "Original Survey Data" sheet on page 4 of the Activity Instructions. It is recommended that instructors prepare a link to this spreadsheet to make it easier for students to access.

At the start of the class session, instructors should prompt the students to form their teams of four to five members or as the instructor decides to organize students. The

TABLE 1 The composition of the pom regional species pool for the biogeography activity

| OTU no. | OTU descriptor | Descriptor | Total in pompom pool |
|---------|----------------------|---|----------------------|
| 1 | Small sparkly green | Abundant, persistent (cosmopolitan) | 150 |
| 2 | Small sparkly white | Abundant, patchy | 200 |
| 3 | Small purple | Competitive exclusion: med dom. but rare when OTU 10 is present | 45 |
| 4 | Small black | Medium abundance, patchy, inverse of OTU 1 | 60 |
| 5 | Small green | Medium abundance, gradient increase | 35 |
| 6 | Small yellow | Medium abundance, gradient decrease | 50 |
| 7 | Small blue | Medium abundance, persistent | 60 |
| 8 | Small red | Medium abundance, categorical (A–F, G–O) patchy | 50 |
| 9 | Small orange | Medium abundance, gradient unimodal | 35 |
| 10 | Small pink | Abundant in three communities/categorical G–O, otherwise rare (endemic) | 75 |
| 11 | Small brown | Rare persistent (cosmopolitan) | 30 |
| 12 | Small white | Rare patchy correlated with black | 30 |
| 13 | Large sparkly orange | Rare persistent | 12 |
| 14 | Large sparkly yellow | Rare but present entirely in only one community (endemic) | 17 |
| 15 | Large sparkly green | Rare persistent (cosmopolitan) | 15 |
| 16 | Large sparkly pink | Rare across two communities categorical G–O (endemic) | 15 |
| 17 | Large sparkly white | Rare patchy | 10 |
| 18 | Large sparkly purple | Rare patchy | 7 |
| 19 | Large sparkly blue | Rare singleton | 10 |
| 20 | Large sparkly red | Rare singleton | 10 |

instructor should introduce the activity and hand out the printed Worksheets (Appendix 4), again 2+ copies per team.

The first step in the activity is for students to take 10 minutes to collaboratively complete the first page of the Worksheet: The Preamble. This page prompts students to define each of the key terms covered in the lecture that will be applied during the activity. Instructors should take 5 minutes to review the definitions of each term to ensure all teams have correct definitions to reference throughout the activity.

Second, the instructor will distribute one copy of the Activity Instructions and the Activity Data Sheet to each team and have students begin reading the instructions. While they read, the instructor will bring out the prepared community pool of pompoms, mix the pool in front of students, evenly divide the pool into the containers, and tuck a random Environment Card into each container. The instructor will then distribute a random container to each team.

Third, the students will work through the activity, with the instructor lightly guiding teams through each step (see Fig. 1), especially to coordinate when the “Windstorm” step takes place so that all teams exchange microbes at approximately the same time and not disrupting each other. At the end of the activity, the instructor will provide students with the link to the combined class data spreadsheet, and one student from each team will enter the OTU abundance values from their “Finish” column into the appropriate column for their environment. In the meantime, the rest of the team can return their pompoms to the containers and return the containers and Environment Cards to the instructor.

At this point, student teams can begin completing part 2 of the Worksheet. The instructor should lightly monitor student teams, checking in with teams that seem stuck, quiet, or particularly divided. Depending on the class timing, student progress, and perceived difficulty, the instructor can choose whether to pause teams for class-wide discussion at the end of each of the three pages (for a limited time or for students who are struggling) or allow students to progress through the worksheet and discuss the entire worksheet at the end of the class session.

For the instructor, the cleanup involves recombining the pompoms and Environment Cards from the containers. If the students did write on their Activity Instructions, those can be collected for re-use. Students may retain their completed worksheets unless the

instructor wants to grade them. The instructor should later provide students with the Worksheet Answer Key for review and exam preparation.

Tips and tricks

If there are fewer than 15 teams, remove environments A, B, and O from the pool because they are redundant with other environments. Environments A, B, and O are on a separate page from environments C to N to easily exclude them during printing.

We recommend printing the Activity Instructions, Data Sheet, and Worksheet as single sided. This ensures that students are not trying to enter their classroom data on the other side of the same piece of paper as the instructions or questions.

This activity works best when students can co-locate together to discuss. If the classroom has rigid row-style seating, plan to supply an additional copy of the Activity Instructions and Worksheet or provide digital copies of the materials and prompt students with laptops to refer to the digital versions.

We used craft poms, but any collection of small objects could be substituted to assemble the communities and regional species pool, for example: buttons, shells, stickers, etc. We originally tried candies (allergen caution) but found that some students ate some of the community members before the end of the activity, which could impact the teams' resulting species distributions.

Activity timing (80-minute class)

1. (Worksheet) Preamble Review—10 minutes; 5 minutes for students to work in teams to review concepts, 5 minutes for the instructor to review answers and answer questions.
2. (Activity) part 1: The Experiment—15 minutes; get students started reading the instructions, while the instructor mixes and distributes the pompoms.
3. (Worksheet) part 2: Analysis and Synthesis—teams should work for 30 minutes with the instructor circulating between teams to monitor progress and intervene in teams getting stuck on a topic too long.
4. Discussion of part 2—25 minutes; instructor leads teams in sharing their answers and sharing their logic.

Suggestions for determining student learning

The students and the instructor can determine student learning through formative and summative assessments. The classroom discussions after the Preamble Review and the Analysis and Synthesis parts of the activity enabled students to self-assess their understanding of the concepts and clarify misconceptions at multiple stages. In addition, while the completed worksheets were not graded for correctness, we found it informative to review students' work for accuracy and completeness (Appendix 6). Combined with our notes on the classroom discussions during the activity, this review process informed minor reorganization of the worksheet, suggested areas for improvement in student preparedness for the activity, and provided feedback on our time management. We gave students feedback on their worksheets and a copy of the worksheet key to support their exam preparation. We based this study on several exam questions and used these same questions to assess the impact of the activity on student learning (Appendix 7). The alignment between the learning objectives, activity worksheet prompts, and exam questions is provided in Table 2. In our study, these were administered once as a summative assessment in the subsequent exam, but these questions could also be administered before the activity to assess established knowledge.

Sample data

Anonymous data and R code used for visualization and analyses are provided on GitHub (<https://github.com/natalie-vandepol/BiogeographyActivity>). Two examples of student

TABLE 2 Alignment between learning objectives and assessment activities

| Learning objective | Worksheet questions | Exam questions |
|---|---------------------|---|
| Define the following terms: biogeography, species-area relationships, neutral models, cosmopolitan, and endemic | Preamble | F1_M1, F2_M2a, F3_M2b, F4_M2c, M5a, M5b, M6 |
| Relate spatial observational effort to patterns of microbial diversity | Part 2, Q7a–7c | F1_M1, F2_M2a, F3_M2b, F4_M2c |
| Hypothesize how microbial diversity may change across environmental gradients and provide examples | Part 2, Q6 | F2_M2a, F3_M2b, F4_M2c, F8_M4 |
| Use models of abundance occupancy to identify taxa that fit the neutral expectation from and those that do not | Part 2, Q9a–9c | F5_M3a, F6_M3b, F7_M3c, M5a, M5b, M6 |
| Explain how the environmental heterogeneity contributes to patterns of microbial populations and communities over space | Part 2, Q5, Q6, Q7c | F2_M2a, F2_M2b, F8_M4 |

responses to the questions in part 2 of the Worksheet are provided in Appendix 6. These two examples highlight some of the variations that can occur in student responses.

Safety issues

There are no safety issues beyond COVID-19 exposure management due to teamwork and material handling associated with this course. A remote teaching modification is provided in the discussion.

DISCUSSION

Field testing

We have used this activity in four semesters of Microbial Ecology (MMG 425) course at Michigan State University, an offering within the Department of Microbiology and Molecular Genetics in the College of Natural Sciences. MMG 425 was an elective for Microbiology and Molecular Genetics majors, a requirement for the MMG majors who opt into the Environmental Microbiology track, and Biosystems Engineering majors. It was also taken as an elective by other majors, including crop and soil sciences, geosciences, environmental engineering, food safety and toxicology, and environmental sciences. It enrolled between 40 and 65 students and met twice a week for 80 minutes each class period. Most of the undergraduates in MMG 425 were juniors or seniors, though there was an occasional sophomore, and the breakdown was ~60%–75% MMG majors with ~20%–30% engineering majors and ~5%–15% other. It was also often taken by first-year graduate students. Most of these graduate students were pursuing Master's degrees in crop and soil sciences or related disciplines, but some were PhD track. Notably, there were no prerequisites for MMG 425 due to the broad and interdisciplinary representation of the enrolled students. This simultaneously offered a challenge and potential for learning enrichment because the students arrived with sometimes very different disciplinary knowledge and cultures.

This activity was created to respond to our initial observation of student underperformance on the biogeography content of the final exam in spring 2018 (SS18) (semesters and class sizes indicated in Table 3). The activity was first introduced in the spring semester of 2019 (SS19) and then continued into the fall semester of 2019 (FS19), fall 2020 (FS20, *virtual offering*), and fall 2021 (FS21). Primary field-testing data were collected in SS19 and fall FS19. Students were informed of the collection of standard classroom data for activity assessment, and data gathering was approved by the Michigan State University Institutional Review Board (Office of Regulatory Affairs Human Research Protection Program, Study ID STUDY00001727) with exempt determination under 45 CFR 46.104(d) 1.

Instructor observations

In both SS19 and FS19, we observed student satisfaction with the activity, noting smiles, laughter, and enthusiastic discussion. Some teams divided up responsibilities between

TABLE 3 Summary of class sizes and their participation in the student data reported here

| Semester | Students enrolled | Activity presented | Data collected | Students who took the exam |
|----------|-------------------|--------------------|----------------|----------------------------|
| SS18 | 58 | No | Yes | 58 |
| SS19 | 63 | Yes | Yes | 63 |
| FS19 | 46 | Yes | Yes | 44 |
| FS20 | 49 | Yes | No | NA ^a |
| FS21 | 39 | Yes | No | NA |

^aNA, not applicable.

members for the simulation and then worked together to answer the discussion questions. It was often evident which team members had watched/attended the lecture before the class session. Still, most students had a laptop to access the prior posted course materials and search the internet for definitions, which enabled students to progress and succeed even without having watched the lecture.

Immediate student feedback: Post-Its

In SS19 and FS19, at the end of the activity, we collected Post-It notes on which students anonymously responded to two prompts:

1. What (about the learning activity) increased your understanding?
2. What (concepts) are you still confused about?

This anonymous Post-It feedback was largely positive. Most students reported an increased understanding of biogeography terms, particularly definitions (Table 4). Most lingering confusion focused on the details of the neutral model and the graphical representation thereof. The activity particularly stressed that endemism/cosmopolitanism strictly described occupancy, which was reflected in the proportion of responses that mentioned both subjects.

Evidence of student learning

Worksheet responses

The worksheets were noted as complete or incomplete, and personalized feedback was given to build relationships and establish instructor presence. This allowed us to informally assess where students seemed to have struggled (if anything was crossed out) or if a particular team had short or wrong answers or had not completed the worksheet.

Exam performance

The objective of this activity is to increase student understanding of concepts in microbial biogeography and dispersal. The exam data gathered in testing this activity supported the hypothesis that observing a simulated community over time and applying the course concepts to analyze simulation data would improve student performance on exam questions.

Several exam questions unaffected by the intervention were used to compare students' "baseline performance" between semesters. A large difference in baseline performance would indicate that we should normalize the scores on exam questions related to the intervention. We found that baseline exam performance decreased on the SS19 exam compared to the pre-intervention SS18 exam, while preliminary tests significantly increased performance on the biogeography exam questions. Since we were only interested in determining whether student performance increased, it was deemed unnecessary to inflate the improvement in scores by normalizing the data between the semesters. We did not assess baseline exam performance in FS19.

SS18 was a non-cumulative final exam, whereas SS19 and FS19 were midterm exams. There were several changes necessary for this adjustment, including some

TABLE 4 Summary of student feedback^a

| Year | Prompt | Endemism/cosmopolitanism | Neutral model and abundance/occupancy | Environmental selection | Other |
|------|-----------------------------|--------------------------|---------------------------------------|-------------------------|-------|
| SS19 | Q1: Increased understanding | 13 | 23 | 1 | 9 |
| | Q2: Still confused | 1 | 18 | 3 | 3 |
| FS19 | Q1: Increased understanding | 7 | 20 | 1 | 6 |
| | Q2: Still confused | 0 | 12 | 2 | 10 |

^aAfter the activity, we asked students for anonymous feedback on Post-It notes. Values indicate the number of responses associated with each main biogeography subject, and "Other" indicates that the response was not specific to any of the categories or was altogether unclear.

recombination of questions and the distribution of question versions between two exam versions: F2-4 became M2a/b/c and F5-7 became M3a/b/c, where F indicates the final exam version, and M indicates the midterm exam version of each question (Appendix S7). The activity described here also inspired two new exam questions (M5 and M6. This meant that, while all 58 students in FS18 answered all the questions, only about half of the students in SS19 and FS19 answered each of questions M2a or M2b, M3a and M3b or M3c, and M5a or M5b (Table 5). Questions M1, M3, M5, and M6 are about the neutral model and the underlying principles of abundance and occupancy. Question M2 is about endemism and cosmopolitanism. Question M4 is about how environmental gradients shape microbial diversity.

For questions M1, M2a, M2b, M3a, M3b, and M3c, we saw a statistically significant increase (Wilcoxon rank sum test, $P < 0.08$) in mean percent score in the semesters with the activity (SS19 and FS19) as compared to SS18 (Fig. 3). M2c and M4 are the two questions that showed no meaningful changes between the semesters, but we noted that these two questions were those on which students historically did not generally struggle. Only question M5a showed any significant difference in mean score between SS19 and FS19. This indicates that the activity presented here significantly impacted student understanding of microbial biogeography concepts, particularly in areas with the lowest scores.

Possible modifications

We modified this activity during the COVID-19 pandemic in the fall semester of 2020, during which Michigan State University had virtual offerings. The typical in-person lectures were converted to four shorter video lectures, and the team materials (worksheet, environment cards, and pom communities) were distributed digitally ahead of the class via Michigan State's course management platform. The pom communities were provided as digital photographs; the instructor created photos of the random pom communities and then also took photos of those that were dispersed into and out of the community (e.g., three photos per team: the original set, a photo of poms that emigrated, and a photo of poms that immigrated). Notably, the same photo of the poms that immigrated away from one pom community was also used as the photo of the poms that emigrated into another, such that there was a complete "dispersal" inclusive of all teams (these pom community photos are available on FigShare at <https://doi.org/10.6084/m9.figshare.24243421.v1>). Teams met with the instructor in a synchronous Zoom session where breakout rooms were employed for teamwork (team members were *a priori* assigned to the same breakout room). For discussion, teams were brought together in the main Zoom room. The instructor moved between breakout rooms to address questions. Because of the extra time needed to accommodate, the

TABLE 5 Number of students who answered each exam question each semester^a

| | Total | F1_M1 | F2_M2a | F3_M2b | F4_M2c | F5_M3a | F6_M3b | F7_M3c | F8_M4 | M5a | M5b | M6 |
|------|-------|-------|--------|--------|--------|--------|--------|--------|-------|-----------------|-----|----|
| SS18 | 58 | 58 | 58 | 58 | 58 | 58 | 58 | 58 | 57 | NA ^b | NA | NA |
| SS19 | 63 | 63 | 33 | 30 | 63 | 33 | 33 | 30 | 63 | 33 | 30 | 63 |
| FS19 | 44 | 43 | 24 | 20 | 44 | 20 | 20 | 23 | 44 | 20 | 24 | 44 |

^aTotal indicates the number of students who took the exam. The values for each question (columns) and each year (rows) are the number of scores represented in Fig. 3 and used in the statistical analyses. Exact prompts for each exam question (e.g., F1_M1) are linked in Appendix 7: Example Exam Questions.

^bNA, not applicable.

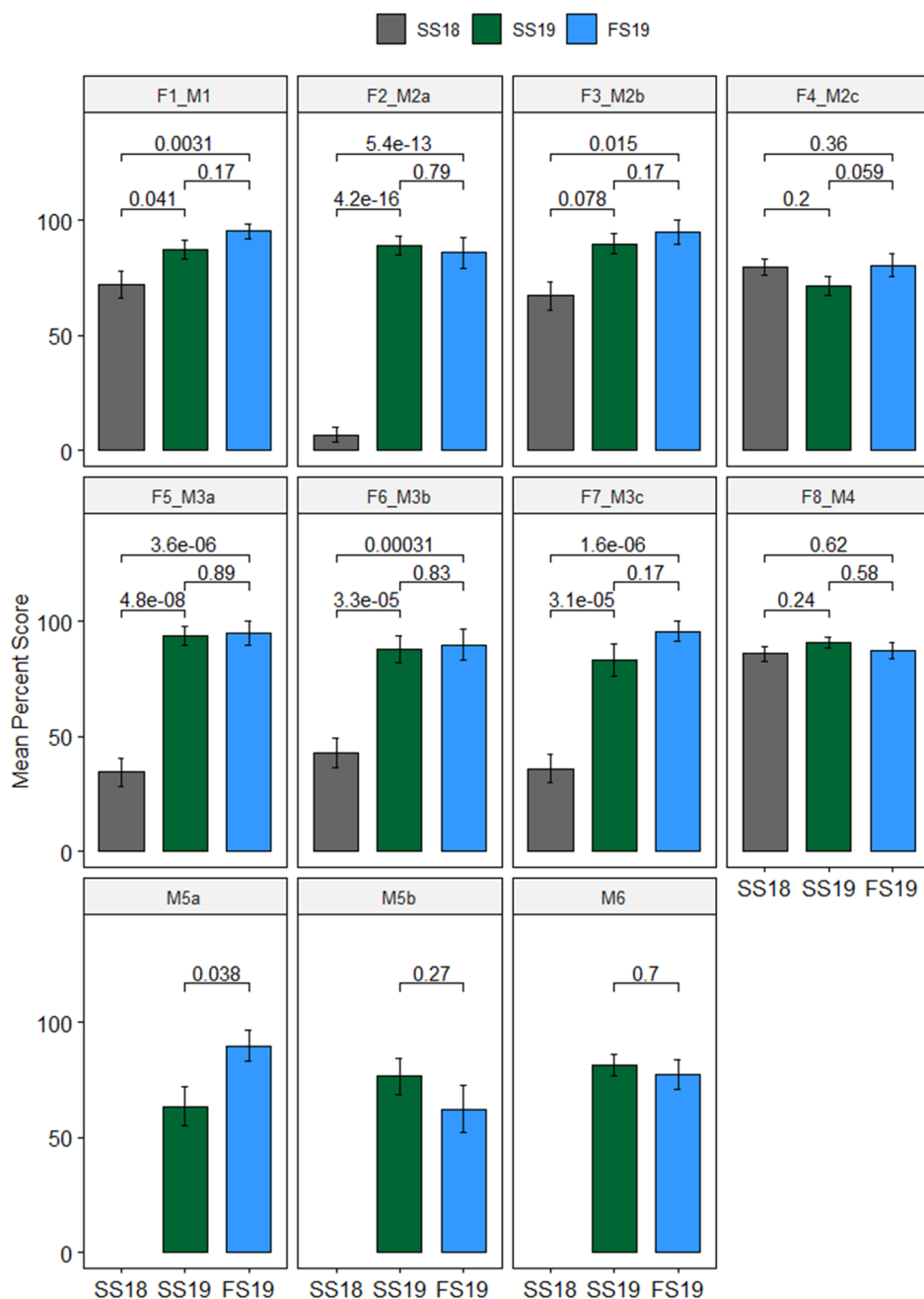


FIG 3 Mean percent score on biogeography exam questions. There is a separate box for each question, labeled by question number. Bars are colored by year, the bar height indicates the mean percent score, and the lines at the top of the bars indicate the standard error. Within each box, the horizontal lines and associated numbers indicate the *P*-value of Wilcoxon rank sum tests between the indicated population means. SS is the spring semester, FS is the fall semester, and the last two digits represent the year of implementation (2018 or 2019).

virtual activity took longer than the usual 80 minutes, and the final class discussion occurred at the beginning of the subsequent synchronous period. This modification demonstrates that the activity is flexible to be broken down into smaller sessions or extended according to instruction needs.

Conclusions

In conclusion, the biogeography activity described here is inexpensive and easy to implement. It provides a forum for students to deeply engage with microbial ecology concepts and practice applying them to classroom data in a way that can meaningfully impact student learning and build quantitative reasoning. The active, collaborative, and reflective teaching methodologies upon which the activity was founded foster a safe, fun, and highly responsive environment where students work with the instructor to explore and learn.

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AUTHOR CONTRIBUTIONS

Natalie S. Vandepol, Conceptualization, Data curation, Formal analysis, Investigation, Visualization, Writing – original draft | Ashley Shade, Conceptualization, Funding acquisition, Investigation, Supervision, Writing – review and editing

DATA AVAILABILITY

Data and analysis code is available at <https://github.com/natalie-vandepol/BiogeographyActivity>.

ETHICS APPROVAL

This study was approved by the Michigan State University Institutional Review Board (IRB) (Office of Regulatory Affairs Human Research Protection Program, Study ID STUDY00001727) with exempt determination under 45 CFR 46.104(d) 1.

ADDITIONAL FILES

The following material is available [online](#).

Supplemental Material

Appendix 1-7 (jmbe00170-23-s0001.pdf). The supplemental appendices provide instructor and classroom materials for printing (Appendix 1: Activity Environment Cards for use in the activity; Appendix 2: Activity instruction sheet for use in the activity; Appendix 3: Blank Activity data sheet for use in the activity; Appendix 4: Blank Worksheet for use in the activity; Appendix 5: Worksheet answer key; Appendix 6: Sample student worksheets to demonstrate potential student responses; Appendix 7: Exam Questions used in our study).

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