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11 Motivation

12	Biological interactions are a predominant way in which students learn about the
13	ecological and evolutionary processes that influence biodiversity. However, most general
14	biology textbooks primarily use animals, reptiles, or invertebrates as case studies to demonstrate
15	the importance of interactions in nature (Uno, 1994; Schussler et al., 2010; Link-Perez et al.,
16	2010). This contrasts with the fact that (1) plants are ubiquitous, and students encounter them
17	regularly in their daily lives, and (2) most interactions that plants rely on happen belowground.
18	Since it can be difficult to present plants (and especially soils) in exciting ways, many students
19	unintentionally cultivate a fauna-centric viewpoint of the natural world (Wandersee & Schussler,
20	2001). To highlight the importance and relevance of plant-soil relationships, we devised a simple
21	role-playing activity suitable for college students.
22	

23 Context

24 Research on plant-soil interactions and their importance in ecology and evolution has 25 blossomed in recent decades. Specifically, feedbacks occur when plants condition soil properties 26 and, in return, are affected by the conditioned soils (Bever, 1994). Negative feedbacks reduce the 27 performance of individuals of the same species relative to other species, resulting in negative 28 frequency-dependent selection (Packer & Clay, 2000, Mangan et al., 2010). Positive feedbacks 29 encourage conspecifics to thrive in their respective soils more than heterospecifics, leading to the 30 monodominance of single species (e.g., invasive species). These reciprocal interactions can 31 shape the non-random assembly of plant communities (Bever 1994; van der Putten 2013).

32

33 **Purpose**

34	The activity has two main purposes: (1) to engage students in a more active interpretation
35	and discussion of the interactions between plants and soils, and (2) to connect these interactions
36	to larger concepts of drivers of biodiversity and ecosystem function. This aligns with a core
37	concept in Biology (sensu AAAS, 2011): living systems are interconnected and interacting.
38	Plant-soil interactions provide a rich example of the interconnectedness of living systems, but are
39	hidden from everyday view and overshadowed by more popular teaching examples. By actively
40	role-playing plants and soils, students can see how these interactions operate in nature.
41	
42	Activity description
43	The primary learning objective of this activity is for students to recognize how plant-soil
44	interactions alter patterns of plant community diversity. This activity simulates how plant-
45	soil feedbacks influence species abundance and richness over time. It is recommended that the
46	game first be played in Negative Mode. A Positive Mode variation is introduced at the end of
47	this description.
48	Negative Mode demonstrates how negative plant-soil feedbacks promote and maintain
49	diversity. When the same plant species and soil properties are matched, the plant dies.
50	Oppositely, plants survive when species and conditioned soils are mismatched. For example, if a
51	Spruce interacts with soil that has been previously conditioned by Spruce, that plant will die. But
52	if the soil has been conditioned by Pine, Ash, or Ailanthus species, the Spruce will survive.
53	The directions for setup are as follows:
54	(1) Split the class so that there are equal numbers of plant and soil players (Fig. 1a). Clear
55	enough space in the room so that plant and soil players can stand in two opposing
56	lines with no obstacles between the groups (Fig. 1b). Soil players each receive one

57	blank notecard and paperclip. Include a pile of paper cutouts of the different plant
58	species (3x the total amount of plant players for each species) to serve as the species
59	pool, as well as a separate discard pile for when plants die and are not returned to the
60	species pool.
61	(2) Each plant player randomly draws one species from the species pool and returns to
62	the line opposing soil players. Record the abundance of each plant species in the
63	community at this initial time point (T_0) . These abundances are recorded on multiple
64	graphs (one graph for each time point; Fig. 2a). Note: the game can be purposefully
65	set at different levels of diversity at T_0 .
66	After set-up, the gameplay begins:
67	(3) Plant players approach a random soil player to begin the conditioning phase that
68	determines how plants change the physical, chemical, and biotic components of their
69	soils based on traits related to their identity. For example, Ash leaves have lower
70	carbon (C) to nitrogen (N) ratios than Spruce needles, which affects the quality of
71	litter inputs to the soil and structures decomposer communities. To simulate
72	conditioning, plant players hand their species to soil players, and soil players
73	paperclip the species behind their soil card to hide the species that conditioned them.
74	(4) Plant players then randomly draw another species from the species pool, form a new
75	line opposing the now-conditioned soil players, and interact with a random soil
76	player. It is important that plant players do not know the conditioned status of soil
77	players before interacting with them (just as tree seedlings cannot preferentially
78	choose more hospitable soil locations in a forest). In this interaction, plants approach

79	soils and show their species identity; in response, soils reveal to the plants what
80	species they have been conditioned with. If they match, the plant dies.
81	(5) Plants that survive remain standing next to their respective soil player (no other plant
82	can interact with soils that have a surviving plant). Plants that die discard their species
83	in a separate pile (i.e., their genes do not get returned to the gene pool), before
84	randomly re-drawing species from the species pool to interact with the remaining
85	unmatched soil players. This gameplay continues until all plants are surviving and
86	matched with a soil player. At this point, pause the game to record diversity with
87	species' abundances (Fig. 1b).
88	(6) Once diversity has been recorded, plants re-condition soils with their current species
89	identity, making soil players clip the new species over their previous species before
90	the next round (repeating Step 3). Again, the new conditioned statuses of soils should
91	be hidden. Repeat steps 4-6 until you have measured diversity for multiple
92	generations (T_0 – T_4 , or longer).
93	
94	Positive Mode is a variation of the game with rules to show how positive plant-soil
95	feedbacks are unstable and reduce diversity as one species becomes monodominant (e.g.,
96	invasion success through allelopathy). To play in Positive Mode, one plant species must be
97	designated to have positive soil interactions, while all other plant species continue playing in
98	Negative Mode. This designated species survives in all soil types conditioned by all species
99	(including its own), and no other plant species can survive in soils conditioned by the designated
100	species (Fig. 1b). For example, Ailanthus is an invasive tree species that produces toxic

101 chemicals that inhibit the growth of nearby plants (Heisey 1990). Therefore, if Ailanthus were

102 designated to have positive interactions, they would survive in any soil no matter what plant

103 species conditioned that soil. In addition, Pine, Spruce and Ash species would die if they interact

104 with Ailanthus-conditioned soil or their respective soils.

- 105
- 106

Assessment, feedback, and suggestions

107 For a follow-up activity, we asked students to relate the direction of plant-soil feedbacks 108 (positive or negative) to the abundance of specific plant species and total species richness (using 109 results from the primary literature; Packer & Clay, 2000, Bais et al., 2003, Klironomos, 2002, 110 Mangan et al., 2010, Bennett et al. 2017). Students successfully predicted that species with 111 negative feedbacks would be rarer in communities that could sustain a greater number of total 112 species, and that species with positive plant-soil interactions would be more abundant in less 113 diverse communities.

114 We also asked the following question before and after the activity: "What do plant-soil 115 feedbacks make you think of?". Responses that included the words "fungi" or "mycorrhizae" 116 increased 75%, and the word "diversity" appeared only in post-activity responses (7 out of 26 117 responses) (Fig. 2b). This suggests that students began to recognize how the nature of plant-soil 118 relationships relate to biodiversity patterns.

119 The activity takes ~30 minutes to complete and preceded a brief lecture and small group 120 work in an upper-level Ecology course (24 students, 18-25 years old). Depending on student 121 level and module topic, instructors using this activity could discuss a range of mechanisms, such 122 as soil nutrient depletion by the plant, mutualistic benefits from mycorrhizal fungi, or build-up of 123 soil-borne pathogens. Since plant-soil interactions have been explored in a variety of areas (van 124 der Putten et al. 2013), the activity can be uniquely paired with different biology topics. For

introductory students, shapes could be used in place of species to focus on the mechanics offeedback loops in nature.

127 This activity may be most applicable for small class sizes (20-40 students). In larger 128 classes, this activity could be implemented as a demonstration with student volunteers or during 129 discussion/laboratory sections. We found it best to use paper cutouts and notecards to drive home 130 the role-playing aspects of the game. We have provided resources for teachers to print the 131 species used in the current example (https://github.com/mvannuland/Species supplies), but the 132 activity is amenable to any suite of species (4-5 plant species is the appropriate number for a 133 small class). With an inexpensive, time-efficient, and engaging activity, we hope to enable 134 teachers to encourage student understanding of prolific, but overlooked, forms of biological 135 interactions that impact the diversity and functioning of ecosystems.

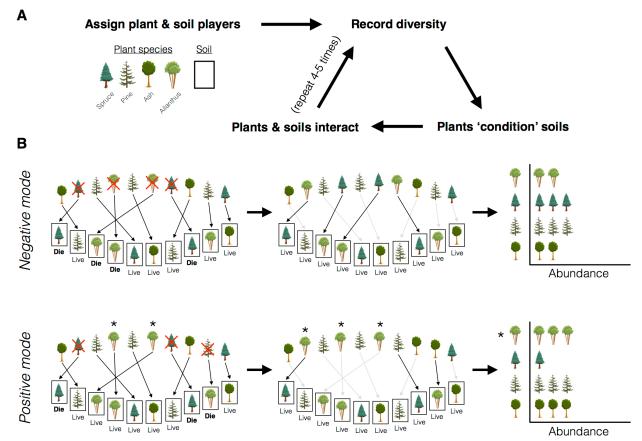
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Figure 1. How to perform the activity. (A) The flow diagram outlines the general approach to the activity. The game is based on many random 1-on-1 interactions between plant and soil

172 the activity. The game is based on many random 1-on-1 interactions between plant and solit players. (B) The outcome of plant-soil interactions depend on the mode and identities of both

174 plant and soil players. Plants that live remain matched with their soils (players stand next to one

another; grey arrows). Plants that die discard their species, draw a new species from the species

176 pool, and interact with any unmatched soil. In negative mode, plants die when they interact with

soils conditioned by the same species (i.e., survival occurs when plants and soils are

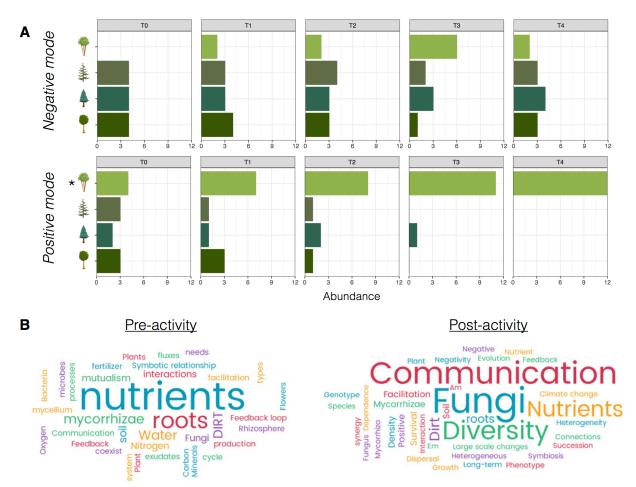
mismatched). In positive mode, select one plant species that will have positive interactions (e.g.,

179 Ailanthus species marked with asteriks). This species survives in all soil types, and no other

180 species can survive in Ailanthus-conditioned soil. Plant species' abundances are recorded once

all plants are living to show how the species' abundance and community richness is shaped by

182 plant-soil interactions.



183

184 Figure 2. Evidence that the activity is successful and effective. (A) Modeling plant-soil 185 interactions with the role-playing activity successfully depicted how negative interactions promote community diversity and stability, while positive interactions decrease diversity and 186 187 disrupt communities. In negative mode, we purposefully set the plant community to have lower diversity (3 species) than the total number of species in the species pool (4 species). After one 188 generation (T_0-T_1) , students could see how negative plant-soil interactions increased plant 189 190 diversity with the addition of Ailanthus into the community. In positive mode, plant community 191 diversity abruptly declined as Ailanthus (an invasive tree species denoted with the asterisk) 192 began conditioning a greater number of soil players that allowed them to persist and inhibited the 193 survival of other species. Results are from a class of 24 undergraduates in an advanced ecology 194 course (diversity was recorded on a whiteboard with the whole class at each time step and broad 195 patterns were discussed when the activity ended). (B) Student responses when asked "What do plant-soil feedbacks make you think of?" pre- and post-activity and discussion. Word sizes 196 197 reflect their total prevalence in the class responses. Overall, these responses show that the 198 activity improved their understanding of how plant-soil interactions relate to patterns of 199 biodiversity.