

# Species Interactions Limit the Predictability of Community Responses to Environmental Change

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**ABSTRACT:** Predicting how ecological communities will respond to environmental change is challenging but highly relevant in this era of global change. Ecologists commonly use current spatial relationships between species and environmental conditions to make predictions about the future. This assumes that species will track conditions by shifting their distributions. However, theory and experimental evidence suggest that species interactions prevent communities from predictably tracking temporal changes in environmental conditions on the basis of current spatial relationships between species and environmental gradients. We tested this hypothesis by assessing the dynamics of protist species in replicated two-patch microcosm landscapes that experienced different regimes of spatial and temporal environmental heterogeneity (light vs. dark). Populations were kept in monocultures or polycultures to assess the effect of species interactions. In monocultures, abundances were predictable on the basis of current environmental conditions, regardless of whether the populations had experienced temporal environmental change. But in polycultures, abundances also depended on the history of the environmental conditions experienced. This suggests that because of species interactions, communities should respond differently to spatial versus temporal environmental changes. Thus, species interactions likely reduce the accuracy of predictions about future communities that are based on current spatial relationships between species and the environment.

**Keywords:** species interactions, environmental change, metacommunity, dispersal, protists.

## Introduction

Predicting how ecosystems will be impacted by current and anticipated future environmental changes, including global warming, chemical or light pollution, and urbanization, is a major and pressing challenge. We are already witnessing extinctions, range shifts, and changes in behavior and life history, suggesting that anthropogenic impacts may be causing the widespread reorganization of ecosystems (Sunday et al. 2012; Bartley et al. 2019; Blowes et al. 2019). Unfortunately, we still have limited ability to predict how this reorganization will play out (O'Connor et al. 2012; Urban et al. 2016). This is because dispersal limitation, species interactions, and evolutionary responses make it unlikely that predictions about how ecosystems reorganize will be accurate if they are based purely on correlations between species and current environmental conditions (i.e., space for time predictions).

How a species performs in a given environment depends on both the local environmental conditions and the other species present (Chesson 2000b; Ives and Cardinale 2004). Interactions between species, including resource competition, facilitation, predation, and parasitism, introduce density-dependent feedbacks that can cause the composition of communities to differ from what would be expected purely on the basis of local abiotic conditions (Davis et al. 1998; Soberón and Arroyo-Peña 2017). Furthermore, species' responses to environmental change depend on both the direct effects of abiotic conditions and how other species in the community respond (Suttle et al. 2007; Tylianakis et al. 2008; Gilman et al. 2010). Thus, species interactions may cause communities to differ in composition even if they experience the same environmental

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conditions, particularly if they experienced different environmental conditions in the past (Urban et al. 2012).

While predicting species and community responses to climate change is a major focus of space for time predictions in ecology (e.g., Elith and Leathwick 2009; Thuiller et al. 2012; Urban 2015), the hypothesis that species interactions should preclude accurate predictions should be general to all types of environmental change, including chemical pollution (Saaristo et al. 2018; Fugère et al. 2020), light pollution (Knop et al. 2017), and urbanization (Turrini et al. 2016). Here, we focus on changing light availability across time and space. Light not only is the main resource for all autotrophs but also changes the life history and behavior of a wide range of organisms. Light pollution and changes in light regimes have been identified as a major global change (Gaston et al. 2013), directly disrupting natural communities and affecting species interactions (Knop et al. 2017). As such, changes in environmental light conditions allow us to test general hypotheses about species interactions and environmental change in a context relevant to global change.

If species must shift their distributions to track environmental change, dispersal is necessary and thus may be critical for spatial and temporal responses to environmental change to match (Urban et al. 2016). Low rates of dispersal may allow species to colonize habitats where the environment change makes conditions suitable. Contrastingly, high rates of dispersal can alter the population sizes of species that are already present (Holt 1985), change competitive outcomes (Fox 2007; Thompson and Gonzalez 2017), and homogenize spatial differences in community composition (Amarasekare and Nisbet 2001; Loreau et al. 2003; Davies et al. 2009). Thus, the role of dispersal in determining the response of communities is hypothesized to depend on whether there is turnover in species occupancy across space and whether dispersal is high enough to modify population sizes and homogenize communities across space.

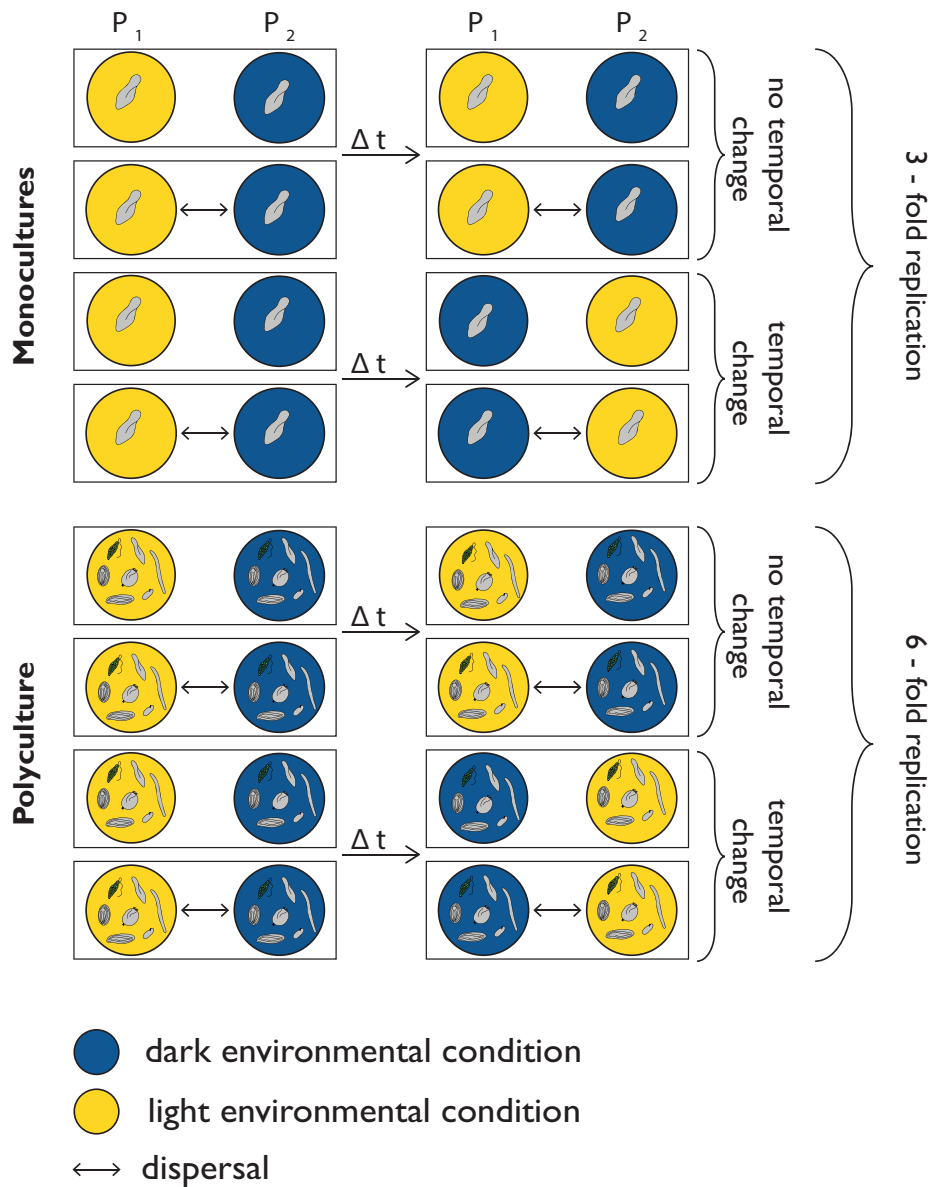
Here, we experimentally tested the hypothesis that species interactions prevent communities from predictably tracking temporal changes in environmental conditions on the basis of current spatial relationships between species and environmental gradients (Davis et al. 1998; Ives and Cardinale 2004). We asked whether interactions between species and low rates of dispersal across an environmentally heterogeneous (light vs. dark) two-patch system affect the degree to which seven-species protist communities respond predictably when local environmental conditions are switched or held constant through time. We assessed the role of species interactions by contrasting community responses when species were present together in polycultures versus when they were kept in their seven respective noninteracting single-species monocultures

but were analyzed as an aggregated community. If species interactions prevent communities from tracking temporal changes in abiotic conditions, then we predicted that (1) initial environmental conditions would strongly influence the final community composition when species interactions were allowed to occur but not when species interactions were prevented and (2) dispersal would be necessary to facilitate such compositional tracking of environmental conditions if there was spatial turnover in species occupancy.

### Material and Methods

We used an aquatic microbial system (protist microcosms) to disentangle the effects of species interactions, dispersal, and temporal change in environmental conditions on local communities exposed to contrasting environments. This model system is well established for testing fundamental ecological questions and is especially well suited to address the effects of environmental change on community dynamics because of its high level of control and replicability (Warren 1996; Petchey et al. 1999; Altermatt et al. 2011; Jacquet et al. 2020). The environmental heterogeneity consisted of a light versus a dark treatment. Protist species have been shown to track these environmental conditions, and they can affect their behavior and population growth dynamics (Giometto et al. 2015, 2017). We measured how community assembly in heterogeneous two-patch metacommunities was shaped by the local conditions and whether and how communities could track a temporal change in this environmental state (fig. 1).

We tested the effect of species interactions by contrasting species' responses to environmental change when they were present in polycultures with when they were in noninteracting single-species monocultures. We aggregated the data from these monoculture populations to simulate the composition of communities without interspecific interactions. Differences in population size between mono- and polyculture treatments were assumed to be due to the lack of interspecific interactions and thus were part of the experimental treatment. We tested the effect of dispersal by repeatedly exchanging small fractions of the populations between the two local habitats, mimicking dispersal, and then compared the results to a no-dispersal control. We also contrasted the responses of communities with and without temporal environmental change so that we could quantify how many of the changes in community composition were due to environmental change compared with temporal fluctuations in population size. Then we assessed the degree to which the communities tracked local changes in environmental conditions on the basis of how closely the composition of the communities that experienced environmental change matched the composition of the communities



**Figure 1:** Schematic representation of experimental setup and treatments. Each two-patch system had two different environmental conditions each (light vs. dark). The environmental conditions either remained constant (no temporal change) or were switched midway through the experiment (temporal change). Two-patch systems were inoculated with either the seven protist species individually (monocultures) or their seven-species polyculture. In a full factorial design, the two patches were connected by dispersal or no dispersal. Each single-species monoculture was replicated three times for each treatment combination. The seven-species polyculture was replicated six times for each treatment combination.

that experienced the corresponding final environmental conditions for the duration of the experiment.

#### *Study Organisms*

We used six freshwater protist species (*Colpidium striatum*, *Euglena gracilis*, *Euplotes aediculatus*, *Paramecium aurelia*, *Spirostomum teres*, and *Tetrahymena pyriformis*) and one

rotifer species (*Cephalodella*) for the experiment. All are hereafter referred to as protists. These protists were kept in a protist pellet (Carolina Biological Supply, Burlington, NC) nutrient medium inoculated with the bacteria *Serratia fonticola*, *Brevibacillus brevis*, and *Bacillus subtilis* as a food source. Two of these species (*E. gracilis* and *E. aediculatus*) are mixotrophs and thus are also able to photosynthesize. All species had been kept in monocultures and kept under

clean laboratory conditions. Before the start of the experiment, we grew all seven protist species to their carrying capacity under optimal conditions. For details of the experimental system and handling procedures, see the laboratory protocols published in Altermatt et al. (2015).

### Experimental Setup

We used six-well polystyrene plates (Axonlab), which were used to inoculate two-patch metapopulations and metacommunities of the seven species. The focal volume was 8 mL. We had single-species metapopulations of all species, as well as the seven-species metacommunity. We added 1.143 mL of each species' stock culture to the respective patches at one-seventh of their carrying capacity. In the single-species patches, we topped up the volume with protist medium to reach the focal volume. All experimental replicates were kept in a randomized order in incubators at 20°C. The experiment was run for a total of 4 weeks, which corresponds to roughly 20–40 generations for our focal species (Carrara et al. 2012; Altermatt et al. 2015). Previous studies have shown that this time frame is sufficiently long for communities to respond to environmental changes, species interactions, and dispersal (Carrara et al. 2015a, 2015b; Pennekamp et al. 2018).

We manipulated the community context (seven metapopulations with one species each vs. the seven-species metacommunity), dispersal (the two patches of the two-patch metapopulations and the metacommunities connected or not connected by dispersal), and the temporal variability of the environmental conditions of the two patches (remaining constant or not). All single-species metapopulations were replicated threefold for each treatment combination, while the seven-species metacommunities were replicated sixfold.

We conducted two dispersal events over the 4-week duration of the experiment, namely, after 2 and 3 weeks (i.e., at the time point of the environmental temporal change treatment and 1 week after). The reciprocal rate of dispersal between the two respective patches was 5% (0.4 mL). Dispersal was density independent and passive, achieved by pipetting the respective volumes between the two well-mixed patches. In the no-dispersal control, we applied the same mixing and pipetting treatment but without spatial inference. Arguably, the chosen rates of dispersal were relatively low, but they matched those of previous work on dispersal effects in protist experiments (e.g., Altermatt et al. 2011). The duration of the experiment was chosen because previous experiments had demonstrated competitive exclusion over a period of a few weeks in patches of the size used (8 mL; see also Carrara et al. 2015a, 2015b; Seymour et al. 2015). We note that extensive work on competitive exclusions in protist experiments (e.g., Cadotte 2007; Fox 2007)

has also been done in larger (40–100-mL) vials, in which competitive exclusion is generally observed only after about 4–6 weeks.

The environmental condition manipulated was light, which is used for photosynthesis by some of the species (*E. gracilis*, *E. aediculatus*) and can trigger behavioral change in many of them. In each two-patch landscape, one patch was either fully illuminated (24 h, LED light, Ledoxon, 4.5 W, 445-lm luminous flux) or completely dark (respective well plates wrapped in aluminum foil). The environmental condition of the two patches (dark vs. light) either remained constant throughout the experiment (no temporal change) or was reversed 2 weeks after the start of the experiment (temporal change). By doing so, we could calculate how communities tracked environmental change (from dark to light or light to dark) and whether and how this tracking was mediated by dispersal.

### Measurements

We recorded and analyzed the species composition, abundance, and diversity in each community (monocultures and polycultures) at weekly intervals using highly resolved video analyses. To do so, we sampled 175  $\mu$ L of each community immediately before the dispersal treatments. The sample was added to a counting chamber mounted on a glass slide, and we recorded a 5-s video (25 frames per second,  $\times 16$  magnification, full light) with a digital ORCA-Flash4.0 camera (C11440-22CU, Hamamatsu Photonics). Of this 175  $\mu$ L, only 34.4  $\mu$ L is visible in the microscope's field of view, so our analyses are based on this volume. We then used this video to identify and quantify the presence and abundance of all seven protist species, closely following a method and R package (BEMOVI) developed and used by Pennekamp et al. (2017). This method links individuals across successive time steps in the videos and calculates a number of morphological and movement features for each individual. It then uses these morphological and movement features in a random forest algorithm. This algorithm is based on decision trees that use binary thresholds to divide the observations into the most possible class at the end node (Pennekamp et al. 2017). The random forest algorithm was trained using the monoculture species (96.1% correct classification rate) and then was applied to classify the identities of all individuals in the polyculture communities (Pennekamp et al. 2017). This method has been demonstrated to be accurate in identifying the identity and abundance of protist species in both monocultures and mixtures (Pennekamp et al. 2015, 2017). The settings for the BEMOVI script were the following: pixel size of 4.05  $\mu$ m, difference lag of 10 frames, thresholds of a 10–255 difference in pixel intensity, minimum particle size of five pixels, maximum particle size of 1,000 pixels, link range of three frames, displacement of 16 pixels, detection frequency of 0.1 s, and median step length of three pixels.



In four replicates, monocultures of *E. gracilis* reached population sizes that were too large for the BEMOVI software to properly link individuals across time steps in the videos, and thus it was not possible to obtain movement statistics. To estimate these populations, we used a linear model to estimate the relationship between the log-transformed number of particles in a single video frame and the log-transformed population sizes estimated as described above for all populations of *E. gracilis* (fig. S1; figs. S1–S5 are available online). We then used this relationship to estimate the missing population sizes using the single-frame output of particles from the BEMOVI analysis.

### Statistical Analysis

We conducted all community composition analyses using Bray-Curtis dissimilarity of relative species abundances. Differences in community composition between treatments were tested using PERMANOVA in the vegan package (Oksanen et al. 2011). We used nonmetric multidimensional scaling (NMDS) to illustrate these compositional differences graphically. We then estimated the degree to which the communities that experienced environmental change tracked those changes in the environment as the Bray-Curtis distance between the final composition of the focal community and the mean composition of the control communities with the corresponding final environment. We tested the effects of the treatments on community tracking using a linear mixed effects model (lme4 package; Bates et al. 2015) with dispersal and final environment as fixed effects and metacommunity as a random effect. All analyses were conducted in R version 3.6.1 (R Development Core Team 2020), and all data and code underlying the results and figures have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.1g1jwstth>; Thompson et al. 2021).

## Results

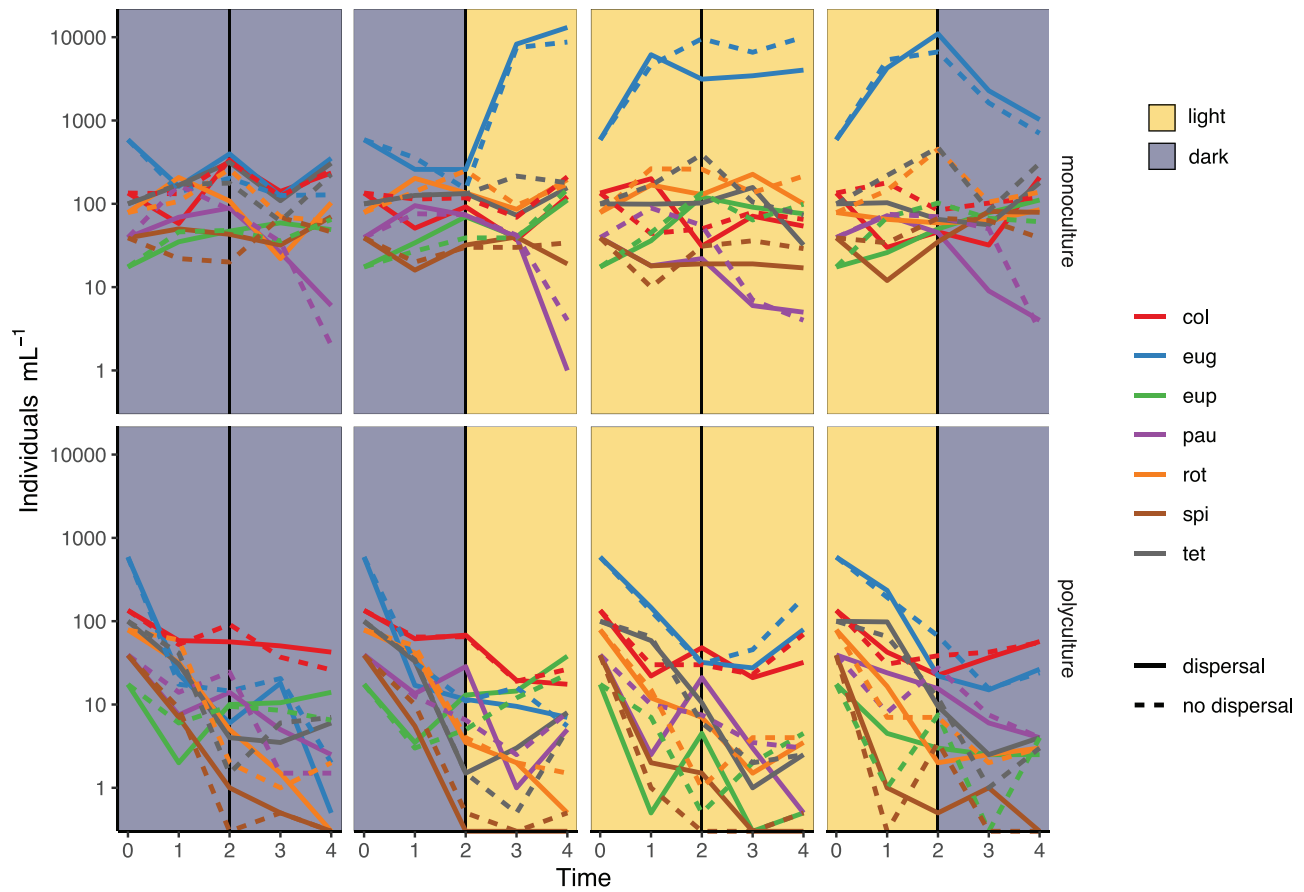
### Community Composition before Environmental Change

The composition of the communities differed between light and dark environments after 2 weeks, before there was an environmental change (environment:  $F_{1,68} = 62.1$ ,  $P < .001$ ; fig. 2). Communities under light had higher abundances of *Euglena gracilis* ( $7,524.0 \pm 1,375.0$  [SE]  $\text{mL}^{-1}$  higher in monoculture,  $29.1 \pm 8.3$  [SE]  $\text{mL}^{-1}$  higher in polyculture) and *Tetrahymena pyriformis* ( $70.2 \pm 74.0$  [SE]  $\text{mL}^{-1}$  higher in monoculture,  $8.46 \pm 1.5$  [SE]  $\text{mL}^{-1}$  higher in polyculture) but lower abundances of *Colpidium striatum* ( $170.0 \pm 66.1$  [SE]  $\text{mL}^{-1}$  lower in monoculture,  $31.2 \pm 8.5$  [SE]  $\text{mL}^{-1}$  lower in polyculture; figs. 2, S2). Other species showed more moderate responses to light (fig. S2).

Interactions between species caused the composition of the monoculture communities to differ from that of the polyculture communities ( $F_{1,68} = 92.6$ ,  $P < .001$ ). Furthermore, the compositional dissimilarity between the monoculture and polyculture communities was greater under light than under dark conditions (environment  $\times$  species interactions:  $F_{1,68} = 35.3$ ,  $P < .001$ ; fig. 2). These compositional differences occurred in part because all species had higher abundances in the monocultures compared with the polycultures (fig. S3). However, the relative abundances also differed between the mono- and polycultures. For example, *E. gracilis* was by far the most abundant in the monoculture communities, whereas *C. striatum* was the most abundant in the polyculture, regardless of light (fig. S3). Although no species was entirely excluded from the polyculture before the environmental change, this was nearly the case for *Spirostomum teres*; it was lost in 54.2% (41.7%) of the dark (light) replicates.

### Community Composition after Environmental Change

Environmental change resulted in significant compositional changes in the communities at the final time point that varied depending on species interactions and the initial environmental conditions (temporal environmental change  $\times$  species interactions  $\times$  initial environment:  $F_{1,68} = 12.1$ ,  $P < .001$ ; figs. 2, 3). These interactive effects on community composition are evident in the differences in the positioning of the communities in NMDS space (fig. 3). In the monocultures, communities that were switched from dark to light (yellow squares) had the same final composition as those that were kept in the light for the entire experiment (yellow circles). This compositional matching did not depend on dispersal. Monoculture communities that were switched from light to dark (blue squares) did not have the same final community composition as those that were kept in the dark for the entire experiment (blue circles). Instead, their composition was intermediate between that of the communities under constant light and those under constant dark, regardless of dispersal. In the polycultures, communities that were switched from dark to light (yellow squares) had a very different final composition from those that were kept in the light for the entire experiment (yellow circles), regardless of dispersal. Furthermore, their final composition was not intermediate between that of the communities under constant light and those under constant dark. Instead, they were more compositionally similar to the communities that remained under constant dark (blue circles), which shared the same initial environment. Polyculture communities that were switched from light to dark (blue squares) also did not have the same final community composition as those that were kept in the dark for the entire experiment (blue



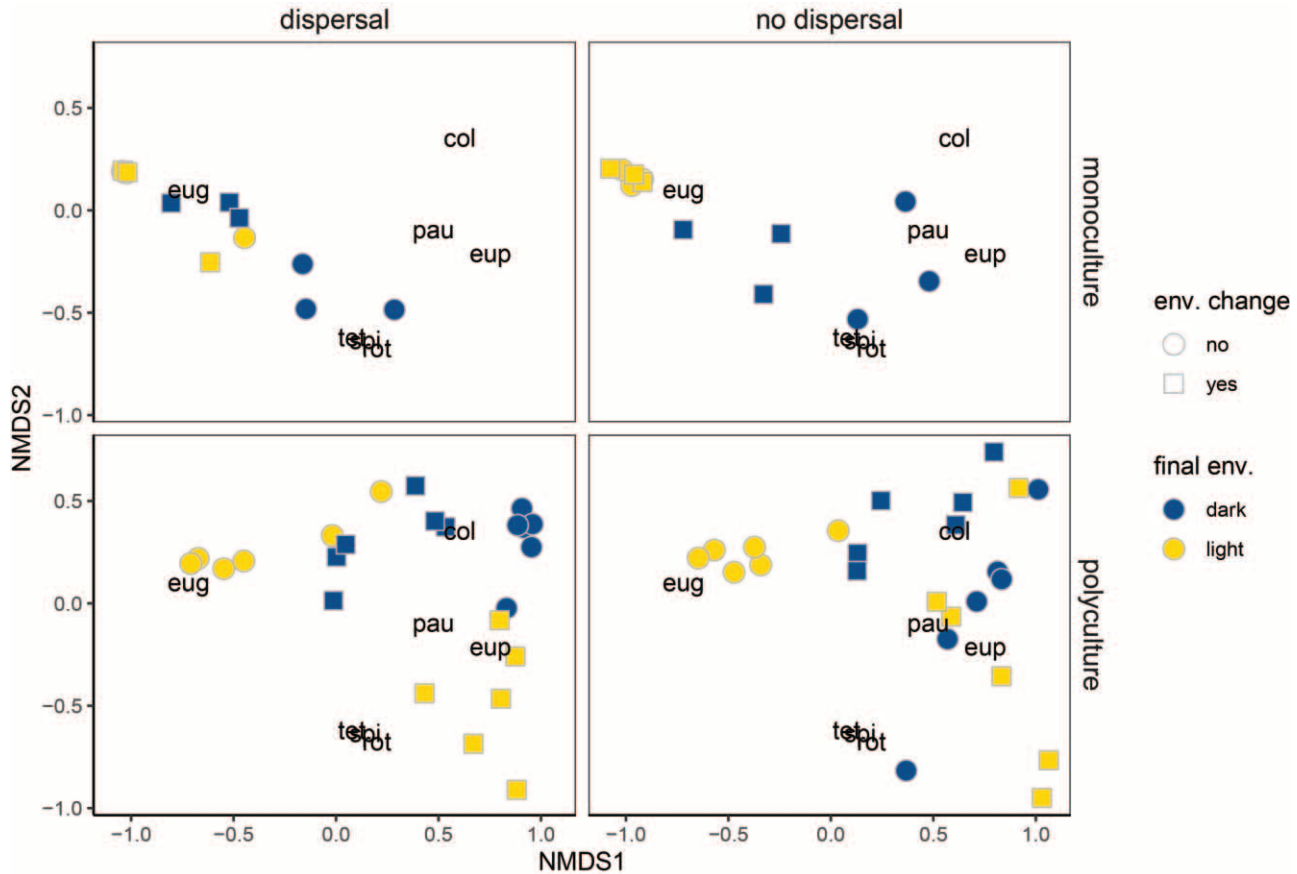
**Figure 2:** Time series of mean abundances of the protist species. The data from the monocultures are shown in the top row, and the data from the polycultures are shown in the bottom row. The environmental conditions at any one time are indicated by the background shading. The leftmost column and the column that is third from the left show treatments where the environment was unchanged. The rightmost column and the column that is second from the left show treatments where the environment was changed midway through the experiment (vertical line). The solid and dashed lines indicate the dispersal and nondispersal treatments, respectively. Variation across replicate treatments is omitted for clarity ( $n = 3$  for monocultures,  $n = 6$  for polycultures), but figure S5 shows the same data with variability measures included. col = *Colpidium striatum*; eug = *Euglena gracilis*; eup = *Euplotes aediculatus*; pau = *Paramecium aurelia*; rot = rotifer (*Cephalodella*); spi = *Spirostomum teres*; tet = *Tetrahymena pyriformis*.

circles). But just as in the monocultures, their composition was intermediate between that of the communities under constant light and those under constant dark.

These differences in community compositional matching to the final environmental conditions are reflected in the distance to the predicted composition metric (fig. 4). Species interactions and the final environmental conditions interactively influenced the degree to which communities tracked environmental conditions ( $F_{1,23} = 86.0$ ,  $P < .001$ ). This interaction occurred because monocultures ( $0.432 \pm 0.04$  SE) and polycultures ( $0.348 \pm 0.03$  SE) had similar tracking when the environment switched from light to dark but tracked the environment very differently when conditions switched from dark to light; the composition of the monocultures was very close to that of the control communities

when conditions switched from dark to light ( $0.077 \pm 0.05$  SE), but the composition of the polycultures was very dissimilar to that of the controls ( $0.680 \pm 0.03$  SE). Dispersal did not alter the degree to which communities tracked environmental conditions ( $F_{1,23} = 0.003$ ,  $P = .960$ ), and the effect of dispersal did not differ depending on species interactions ( $F_{1,23} = 0.510$ ,  $P = .482$ ).

That species interactions had different effects on community composition depending on environmental conditions occurred in part because *E. gracilis* increased in abundance in communities that were changed from dark to light when in monoculture ( $13,921.0 \pm 5,737.0$  [SE]  $\text{mL}^{-1}$ ) but decreased when in polyculture ( $-7,177.0 \pm 2.0$  [SE]  $\text{mL}^{-1}$  higher; figs. 2, S4). However, even though the impact of species interactions is most evident for *E.*



**Figure 3:** Final community composition in nonmetric multidimensional scaling (NMDS) space. Each point indicates the composition of a single replicate community at the final time point of the experiment. The color indicates the final environmental conditions for the treatment. The shape distinguishes treatments with (square) and without (circle) environmental change (following time step 2). The data from the hypothetical seven-species communities based on monocultures are shown in the top row, and the data from the polyculture community are shown in the bottom row ( $n = 3$  for monocultures,  $n = 6$  for polycultures). The three species with overlapping labels are *Tetrahymena pyriformis* (tet), *Spirostomum teres* (spi), and the rotifer *Cephalodella* (rot). col = *Colpidium striatum*; eug = *Euglena gracilis*; eup = *Euplotes aediculatus*; pau = *Paramecium aurelia*.

*gracilis*, our results and conclusions are unchanged when we reanalyze our data excluding this species from the analysis (tables S1–S3, available online).

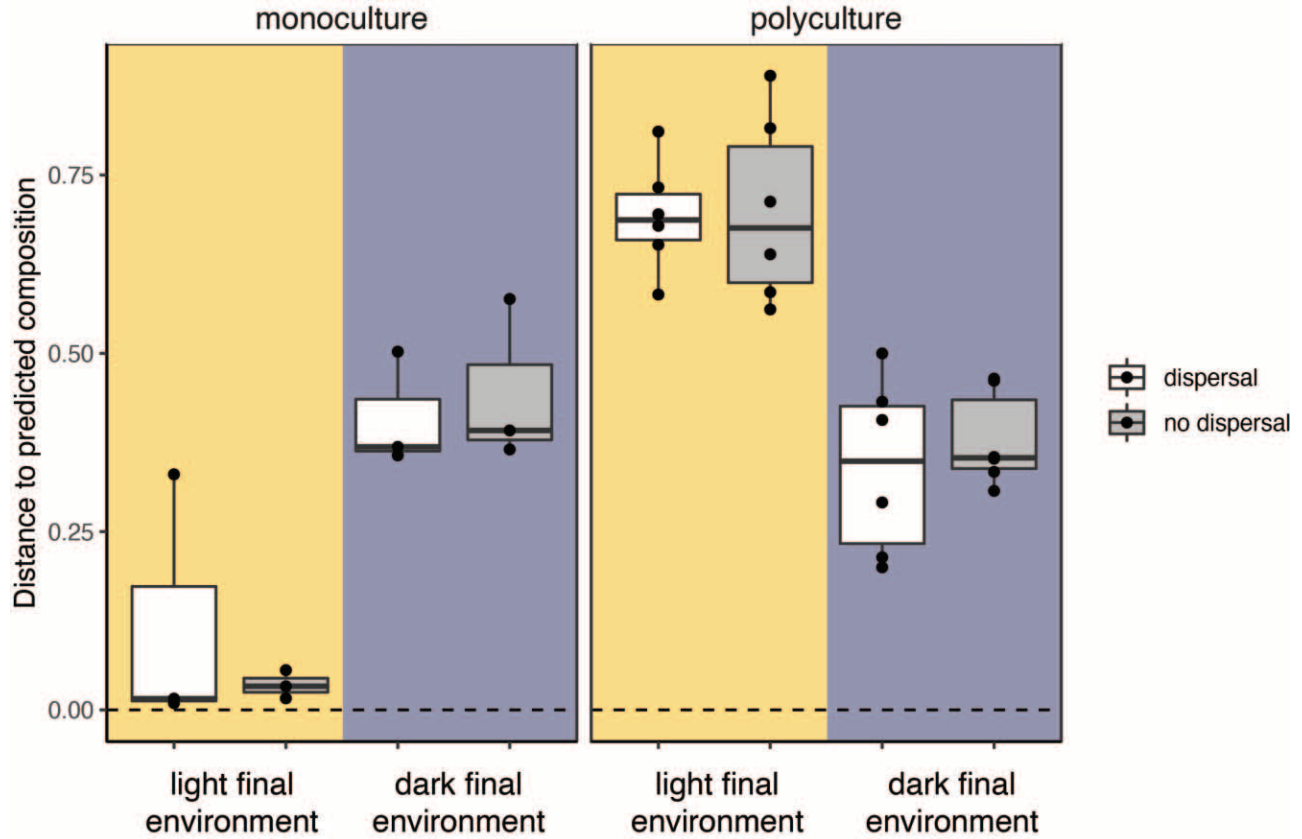
### Discussion

The results of this experiment support the hypothesis that species interactions prevent communities from predictably tracking temporal changes in environmental conditions (Davis et al. 1998; Ives and Cardinale 2004). When species were held in monocultures, their final abundances were predictable on the basis of their current environmental conditions, regardless of whether they experienced an environmental change. But when present with other species, their final abundances depended on whether they had experienced an environmental change and so were not predictable solely on the basis of their current conditions. These

results suggest that interactions between species cause communities to respond differently to temporal versus spatial environmental changes. This means that predictions based on compositional turnover across current spatial environmental gradients are unlikely to provide accurate predictions of how communities will respond to temporal environmental change. While we found no effect of dispersal on community tracking, this was not surprising, as all species were able to persist in both light and dark environments and so colonization was not necessary for them to track environmental changes.

### Why Species Interactions Reduced Community Tracking

In the absence of interspecific interactions, species varied in their abundances in the light and dark environments, and their responses to environmental change were



**Figure 4:** Bray-Curtis distance between the final composition of the treatments experiencing environmental change and mean composition of the unchanged treatments with the same environmental conditions. A distance of zero means that the composition exactly matches that of the unchanged control. White indicates treatments without dispersal, and gray indicates treatments with dispersal. The X-axis indicates the final environment. The hypothetical seven-species communities based on monocultures are shown in the left panel, and the data from the polyculture communities are shown in the right panel. Boxplots indicate the interquartile range, and points indicate the individual replicate values ( $n = 3$  for monocultures,  $n = 6$  for polycultures).

predictable on the basis of these differences. This was most evident for *Euglena gracilis*, which is a mixotrophic species and so reached much higher abundances when exposed to light (fig. 2). Its abundances quickly increased when it was switched from dark to light conditions, reaching numbers that were comparable to those from when it was grown entirely under light (see also Giometto et al. 2015, 2017). When it was switched from dark to light, its abundances decreased, heading toward densities matching those of populations grown entirely in the dark, although they had not declined to those levels by the end of the experiment. The fact that *E. gracilis* tracked the switch from dark to light faster than the switch from light to dark largely explains why, in the monocultures, compositional tracking was greater for this direction of environmental change (fig. 4). However, the fact that our results are qualitatively unchanged (supplemental PDF, available online) when we exclude *E. gracilis* indicates that species interactions prevented compositional tracking for the other species in the community as well.

Interspecific interactions appear to have impeded compositional tracking by preventing individual species from responding to environmental change as they would in monocultures. Notably, the polyculture community that was switched from dark to light was closer in composition to the community that remained in the dark for the duration of the experiment. This contrasts markedly with the communities without biotic interactions, which showed almost perfect compositional tracking when going from dark to light (fig. 4). This difference was most notably due to interspecific interactions preventing *E. gracilis* from increasing in abundance when conditions were switched from dark to light, as it did in the monoculture (fig. 2). Instead, *Colpidium striatum* and *Euplotes aediculatus* remained the most abundant species, as was the case in the community that remained in the dark for the duration of the experiment. While it is not possible to determine the specific mechanism underlying this result from our experiment, it is likely that the suppression of *E. gracilis* occurred through



predation from larger members of the community, such as *E. aediculatus*, as well as through competition for their common bacterial food resource. Future studies could identify this mechanism by repeating the experiment with different combinations of species that include or exclude predators.

These results align with a long history of ecological theory that underpins the expectation that species interactions should prevent species and communities from predictably tracking temporal environmental change. This includes the foundational concept of the fundamental versus realized niche (Hutchinson 1957), which emphasizes that species' responses to environmental variation also depend on interactions between species. More formally, mathematical models based on Lotka-Volterra interactions (Ives and Cardinale 2004; Thompson and Gonzalez 2017), as well as modern coexistence theory (Chesson 2000a; Usinowicz and Levine 2018), suggest that it is the density-dependent feedbacks caused by species interactions that cause community responses to density-independent factors (e.g., light, temperature) to be unpredictable (Thompson et al. 2020). In addition, theory predicts that species interactions can slow the rate at which a community reaches equilibrium (Ives and Carpenter 2007). Thus, it is possible that species interactions may have caused our polyculture communities to converge more slowly on the new equilibrium following environmental change compared with the monoculture communities. However, it is unlikely that this mechanism was the principal difference between our monoculture and polyculture communities because we see that species interactions can change the direction of the response to environmental change for some species. For example, when switched from dark to light, *E. gracilis* increased in abundance in the monoculture but decreased in the polyculture.

To date, the most direct test of this hypothesis comes from Davis et al. (1998), who found that the responses of three species of fruit flies to temperature differed depending on whether they were in monocultures, in mixtures, or with a parasitoid wasp. This study has long served as the key empirical reference for the hypothesis that species interactions can preclude accurate predictions of species distributions under future conditions. By demonstrating a similar outcome with protists, our experiment provides support that the hypothesis is not specific to one type of taxon or interaction. Furthermore, while Davis et al. (1998) focused on species-specific responses, we have shown how biotic interactions scale up to affect the composition of an entire community experiencing environmental change.

The generality of our findings is also consistent with a number of field experiments that have demonstrated the importance of species interactions in determining range limits and responses to environmental change. For example, a meta-analysis of plant translocation experiments found many species (26%) to be capable of persisting in

climates beyond their current range limits (Hargreaves et al. 2014). This suggests that species interactions may be preventing species from occupying the full range of environmental conditions that are suitable for growth. Furthermore, other experiments have shown that species persistence and colonization success along elevational climate gradients are highly dependent on the presence of—and interactions with—other species (Brown and Vellend 2014; Alexander et al. 2015; Usinowicz and Levine 2021).

#### *Why Dispersal Did Not Impact Community Tracking*

In this experiment, all species were able to persist in both light and dark conditions, so community responses to change occurred through changes in relative abundance and not changes in richness. Thus, there was no potential for dispersal to increase community tracking by facilitating colonization. Higher rates of dispersal may have affected community tracking via mass effects, which have been shown to be an important driver of community composition and competitive outcomes in other protist experiments (Donahue et al. 2003; Fox 2007; Davies et al. 2009). But testing the role of mass effects in community tracking was not the goal of our experiment and would have required higher dispersal rates. Repeating this experiment with a range of dispersal rates, including rates higher than those included in this study, would provide a more general understanding of how dispersal and species interactions combine to affect community tracking.

#### *Broader Implications*

Our results suggest that interactions between species likely reduce the accuracy of predictions about future communities that are based on current relationships between species distributions and spatial abiotic gradients. This has important implications for the common practice of using species distribution models (e.g., Thuiller et al. 2009) to make predictions about how species and communities will respond to climate change. Of course, we are not the first to suggest that species interactions are likely to lead to errors when species distribution models are used to make predictions under future conditions (e.g., Davis et al. 1998; Urban et al. 2013). Indeed, modern approaches try to account for species interactions by incorporating co-occurrence patterns, and this can lead to more accurate predictions of current species distributions (Boulangéat et al. 2012; Ovaskainen and Abrego 2020). However, such approaches cannot account for the dynamic nature of species interactions and so would still predict that species should respond similarly to spatial and temporal environmental conditions. Our experimental results demonstrate that this will not necessarily be the case. Interactions between species cause the outcome of environmental change to depend on the past composition of the

community and the order in which species arrive (Fukami 2015). Such temporal dependencies cannot be accounted for using models that rely only on correlations, although it is possible that mechanistic models that incorporate species interactions will do better (Urban et al. 2016). Nevertheless, it is unclear whether we will ever have the types of mechanistic models that will be able to account for the dynamic nature of species interactions. Therefore, the species distribution modeling approach remains one of our most useful tools for making predictions about ecological responses to environmental change. However, we must be aware of its limitations and treat its predictions as approximations rather than accurate predictions of the future (Araújo and Peterson 2012).

#### *Future Directions*

While our experiment provides good support for the hypothesis that species interactions alter the responses of species and communities to environmental change, an important next step is to determine the degree to which the effect of species interactions is context dependent. Future experiments should test the hypothesis that community responses to environmental change can be predicted if we understand how each pair of species in the community interacts. Although quantifying all pairwise species interactions is challenging, it is possible with protist communities (e.g., Carrara et al. 2015b). If species interact as they do in generalized Lotka-Volterra models, then community responses may be predictable (Ives and Cardinale 2004). However, it is likely that species interactions differ depending on the composition of the community (Soliveres et al. 2018). In this case, knowledge about pairwise interactions would be of limited use. Testing this hypothesis is critical for determining whether effort should be spent in developing mechanistic models that incorporate species interactions for predicting biodiversity change (Urban et al. 2016). This hypothesis could be tested by assessing whether species pairs differ in their responses to environmental change depending on the presence of other species.

In our experiment, dispersal was not a strong determinant of community responses to environmental change. However, as we discussed above, this is unlikely to be a general effect. Subsequent studies should test how dispersal mediates community responses to environmental change in a wider range of contexts. We hypothesize that dispersal effects will be strongest when dispersal rates are high and when environmental gradients lead to turnover in community composition. In particular, experiments should contrast a range of dispersal rates, as theory predicts that the effects of dispersal are complex and nonlinear (Loreau et al. 2003; Leibold and Chase 2018; Thompson et al. 2020). Future studies should also allow for species-specific dispersal rates,

as competition colonization dynamics can be important drivers of community dynamics (Cadotte et al. 2006; Cadotte 2007).

#### *Conclusions*

Predicting how ecological communities are responding and reorganizing in this era of global environmental change is a pressing but challenging endeavor (Urban et al. 2016). Predictions that are made on the basis of current spatial relationships between species and abiotic gradients can provide us with expectations of what communities may look like in the future. However, our results suggest that because species interact, responses to temporal change are unlikely to match how communities turn over across spatial gradients. Thus, species interactions result in uncertainty in predictions about how communities will change. This uncertainty should be acknowledged when communicating these predictions, and managers should account for it when making decisions aimed at preserving biodiversity in a changing world.

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#### **Statement of Authorship**

P.T. and F.A. conceived of the study and designed the experiment. S.H. set up and performed the experiment, collected the video samples, performed the preidentification steps of the video analysis, and created the experimental setup diagram (fig. 1). P.T. performed the identification steps of the video analysis, analyzed the data, and created the data figures. P.T. wrote the first draft of the manuscript with methods text from F.A. All authors contributed to edits and revisions.

#### **Data and Code Availability**

All data and code required to reproduce the results of this analysis are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.1g1jwstth>; Thompson et al. 2021) and Zenodo (<https://doi.org/10.5281/zenodo.4131142>).

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