

Variation in the demographic effects of grass-endophyte symbiosis along an aridity gradient

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Abstract

Introduction

Plant-microbe symbioses are widespread and ecologically important. These interactions are famously context-dependent, where the direction and strength of the interaction outcome depends on the environment in which it occurs (Bronstein, 1994; Fowler et al., 2023; Hoeksema and Bruna, 2015). Under biotic stress (e.g., herbivory), endophyte symbiosis can benefit host plants by facilitating the production of secondary compounds that deter feeding or cause direct toxicity, thereby reducing insect growth, survival, and oviposition (Atala et al., 2022; Bastias et al., 2017; Vega, 2008). Similarly under abiotic stress (e.g., drought), symbionts can increase their host tolerance to drought. However, in many plant-microbe interactions, host protection is not guaranteed solely by the presence of a symbionts; rather, the density of the symbiont can determine the effectiveness of this protection (Laughton et al., 2014). Additionally, having a greater endophyte density could lead to high resource exploitation, which may be costly for the host. This cost is often manifested by a reduction in host biomass or reproductive success (Faeth, 2009), particularly under harsh abiotic conditions (Cui et al., 2024). Ultimately, these context-dependent costs and benefits may underlie the observed distribution of host species.

Context-dependence raises the hypothesis that plant-microbe interactions are likely to vary across environmental gradients spanning range-core to range-edge. If the benefits of microbial symbiosis strengthen under environmental stress then symbionts could make range-edge environments more suitable, possibly extending the host's range limits (Allsup et al., 2023; Rudgers et al., 2020). For instance, fungal endophytes improve *Bromus laevipes* populations resistance to drought stress at range edge and thereby expand the species geographic range (Afkhani et al., 2014; David et al., 2019). In contrast if microbial symbiosis is costly for the host at range edge, then symbionts could limit host range (Bennett and Groten, 2022; Benning and Moeller, 2021a,b). Mutualist limitation reduces population fitness and therefore limits range expansion in *Medicago polymorpha* populations (Lopez et al., 2021).

Ecological studies of plant-microbe symbiosis usually study the interaction from the plant's

perspective. Moreover, studies of plant-microbe symbiosis relied on chemical, physical and mechanisms of endophyte fungal exclusion, such as inoculating sterile soil, excluding endophyte fungal hyphae by using fine mesh or rotating cores, and adding fungicide (Bennett and Groten, 2022). Much less is known about how the symbiont respond to environmental variation, and how this might translate to its influence on host performance (Garcia and Gerardo, 2014). Symbionts are promoting their own selfish fitness by manipulating their hosts' life history traits or resistance to stresses caused by abiotic and biotic variation (Giauque et al., 2019; Kazenel et al., 2015; Saikkonen et al., 1998). Therefore overlooking the role of symbionts and their potential cascading effects on the eco-evolutionary population dynamics of host species could lead to inaccurate prediction of host response to current global change.

Understanding how symbiotic interactions are likely to facilitate host persistence in changing environments requires an investigation of the synergistic effects of biotic, abiotic stressors and endophyte presence on individual demographic performance (survival, growth and reproduction) and how that effect can be translated at a population level (Bruno et al., 2003; De Sassi et al., 2006). One of the best ways to perform that investigation is to use common garden experiments along climatic gradient (Schwinning et al., 2022). These common gardens experiments allow the manipulation of variation of biotic and abiotic factors that are likely to change with climate change (eg. temperature, precipitation, endophyte prevalence) and measured species response of such a variation.

Working across a precipitation gradient in the south-central US, we asked how the demographic effects of endophyte symbiosis varied from core to edge of the host range. We also asked how does fungal growth affect host demography from range core to range edge. To answer, these questions, we studied the symbiotic association between a cool-season grass species (*Elymus virginicus*) and its vertically transmitted fungal symbiont *Epichloë elymi*. [Describe ecology and natural history of grass-endophyte interactions]. Our experiment was design to test the following hypotheses:

1. We hypothesized that stress associated with aridity and low precipitation would strengthen

the plant-fungal mutualism, such that the fitness benefits of endophyte symbiosis are maximized at the range edge.

2. We hypothesized that fungal growth in planta varied from range core to range edge. If endophyte growth is limited by host photosynthesis, then environments that are stressful for hosts may correspond to poor endophyte growth. Alternatively, if active regulation by the host is required to keep symbionts “in check”, then environments that are stressful for hosts may correspond to high endophyte growth.

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Statement of Authorship

OEC conceived the experiments, collected the data, and wrote the original draft. GHC provided specimens and analyzed the model. AQE oversaw data analysis and developed the code. All authors reviewed and edited the writing at all stages of revision.

Data and Code Availability

On initial submission, you may use this section to provide a URL for editors and reviewers that is ‘private for peer review’. After acceptance, this section must be updated with correct, working DOIs for data and code deposits (such as in Zenodo, Dryad, or DataVerse). An example statement could resemble the following: All data and code for this work are available from the Dryad Digital Repository, ?).

Appendix A: Additional Methods and Parameters

Fox–dog encounters through the ages

The quick red fox jumps over the lazy brown dog. The quick red fox has always jumped over the lazy brown dog. The quick red fox began jumping over the lazy brown dog in the 19th century and has never ceased from so jumping, as we shall see in figure A1. But there can be surprises (figure A2).

If the order and location of figures is not otherwise clear, feel free to include explanatory dummy text like this:

[Figure A1 goes here.]

[Figure A2 goes here.]

Further insights

Tables in the appendices can appear in the appendix text (see table A1 for an example), unlike appendix figure legends which should be grouped at the end of the document together with the other figure legends.

Table A1: Various rivers, cities, and animals

River	City	Animal
Chicago	Chicago	Raccoon
Des Plaines	Joliet	Coyote
Illinois	Peoria	Cardinal
Kankakee	Bourbonnais	White-tailed deer
Mississippi	Galena	Bald eagle

Note: See table 1 below for further table formatting hints.

Lorem ipsum dolor sit amet, as we have seen in figures A1 and A2.

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Tables

Table 1: Founders of *The American Naturalist*

Early editor	Years with the journal
Alpheus S. Packard Jr.	1867–1886
Frederick W. Putnam	1867–1874
Edward S. Morse	1867–1871
Alpheus Hyatt	1867–1871
Edward Drinker Cope ^a	1878–1897
J. S. Kingsley	1887–1896

Note: Table titles should be short. Further details should go in a ‘notes’ area after the tabular environment, like this.

^a Published the first description of *Dimetrodon*.

Figure legends

Figure 1: Figure legends can be longer than the titles of tables. However, they should not be excessively long—in most cases, they should be no more than 100 words each.

Figure 2: In this way, figure legends can be listed at the end of the document, with references that work, even though the graphic itself should be included for final files after acceptance. Instead, upload the relevant figure files separately to Editorial Manager; Editorial Manager should insert them at the end of the PDF automatically.

Figure A1: *A*, the quick red fox proceeding to jump 20 m straight into the air over not one, but several lazy dogs. *B*, the quick red fox landing gracefully despite the skepticism of naysayers.

Figure A2: The quicker the red fox jumps, the likelier it is to land near an okapi. For further details, see ?.

Video S1: Video legends can follow the same principles as figure legends. Counters should be set and reset so that videos and figures are enumerated separately.