Foliar pathogen dilution due to species richness and phylogenetic dispersion increases productivity in diverse grassland communities

Haley Burrill, Audrey Nelson, Laura Podzikowski, Jim Bever

Background

Pathogen dilution is suggested to be an important benefit of biodiversity, with disease occurrence expected to decline with competent host density (Keesing and Ostfeld 2021). However, pathogen dilution has been controversial and its generality across systems has been questioned. Mixed observations of foliar pathogen dilution suggest that factors such as ecosystem type, plant functional groups, and pathogen dynamics may modify diversity impacts on disease.

Plant composition and environmental context may explain inconsistent observations of pathogen dilution. In particular, phylogenetic relatedness of available plant hosts might affect the variability in observations of foliar pathogen dilution. Since more closely related plant species are more likely to share pathogens, pathogen dilution with species richness should be stronger with phylogenetically diverse plant communities. Further, transmission of foliar pathogens varies with environmental conditions, as many foliar plant pathogens are wind and water dispersed (Scholthof 2007). Increased precipitation, warming and N fertilization have been found to contribute to increased disease in plants. Logically, changes in precipitation and temperature could then alter could affect the dilution of pathogens in more diverse communities.

Evidence of the functional consequences of pathogen dilution on plant community and ecosystem properties is limited. Pathogens can mediate plant species coexistence in plant communities (Crawford et al. 2019, Whitaker et al. 2017, Bever et al. 2015), and pathogen manipulation experiments suggest that they contribute to productivity gains from plant diversity (Wang et al. 2018, Schnitzer et al. 2011, Maron et al. 2011). This suggests that pathogen dilution could be important to overyielding. However, this has only been tested in below-ground pathogens.

Explicit tests of dependence of pathogen dilution on plant phylogenetic diversity and environmental context requires full factorial manipulation experiments with species richness. We designed a study providing a full factorial manipulation of plant species richness (monoculture, 2, 3, 5, and 6 plant species per plot); plant family richness (species all within one plant family (Asteraceae, Fabaceae, or Poaceae) or a mixture of plant families); and precipitation (50% and 150% ambient precipitation). We test this within the tallgrass prairie system including native plant diversity and inoculated with native prairie microbiome (Burrill et al. 2023). We then scored foliar pathogens for all plant species in all plots. We hypothesized that foliar pathogen disease would decrease with plant species richness and plant family richness, further augmented in high precipitation treatments. Finally, we expected foliar pathogen release due to dilution to predict plant community productivity yields.

Methods

Experimental Design

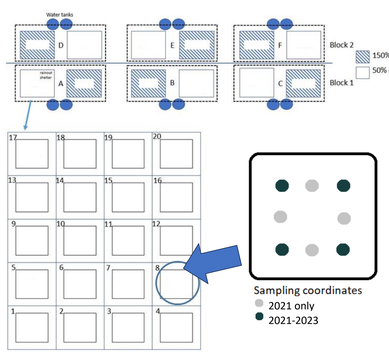
Established in 2018, this field experiment manipulates plant diversity, composition, and precipitation. 18 prairie species were planted in a full factorial manipulation of plant species richness (monoculture, 2, 3, 5, and 6 plant species per plot); family richness with species within one plant family (Asteraceae, Fabaceae, or Poaceae) or family mixture; and 50% or 150% ambient precipitation. Foliar disease was assessed using a scale of severity in years 4 and 5 of the experiment. We hypothesized foliar pathogen dilution would increase 1) with plant species richness, 2) with family richness, 3) with high precipitation; and that 4) foliar pathogen dilution would predict overyielding, as measured by complementarity.

Foliar Disease Scoring

For planted species in each plot, we selected individual stems from the coordinates depicted in Fig. 1. We then took a foliar disease score using a standardized scale:

(1) No signs of pathogen
(2) Leaf discoloration (LD)
(3) 1 spot & LD
(4) 2-3 spots
(5) 25% of plant has spots
(6) 50% of plant has spots
(7) 75% of plant has spots
(8) 95% of plant has spots
(9) Leaves falling off & 95% has spots
(10) Plant is nearly dead

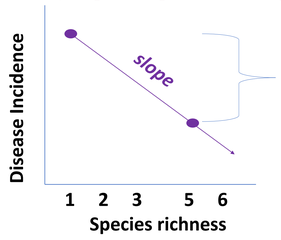
Figure 1 – Plot design layout.



Pathogen Release

Using foliar disease dilution slopes from the regressions of each species, for each plot we summed the difference in disease from the plot's species richness level to monoculture for each species in the plot.

Figure 2 – Depiction of predicted pathogen release calculation, using linear regression for each species.



$$P = \sum_{i=1}^{r} \frac{1}{r}\left(d_{m_i} - d_{r_i}\right)$$

P = predicted pathogen release, d_{m_i} = average disease incidence score of each species in monoculture, d_{r_i} = average disease incidence score of each species at the plot's richness level (r)

Complementarity

Total biomass of individual species in each plot was estimated via cover-strip biomass regressions. Then, total estimated biomass for each plot was used to calculate complementarity, selection effects, and RYT. Complementarity represents the biodiversity effect due to species interactions and is regarded as the most important driver to overyielding (Hector 1998). We used the growing season's aboveground biomass for both years to calculate complementarity effect (CE) for each year. This number is highest when species mixture yields are higher than expectations based on monoculture yields. CE was calculated as:

$$\mathrm{CE} = N \times \overline{\Delta \mathrm{RY}} \times \bar{M}$$

N = plant species richness, ΔRY = deviation from expected relative yield of species in the mixture, M = a species' average monoculture biomass, $\overline{\Delta \mathrm{RY}}$ = the mean change in relative yield for each species in mixture, and $\bar{M}$ = the mean monoculture biomass for each species.

Results

Species Richness Dilution

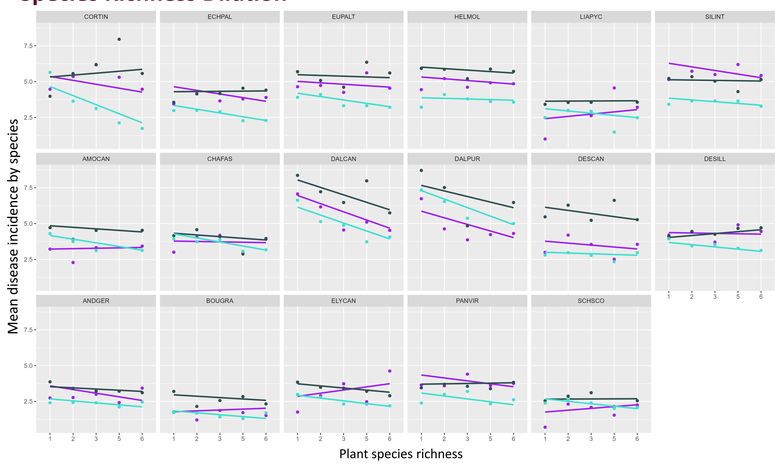


Figure 3 – **Foliar disease dilution with increased plant species richness.** Top row Asteraceae, middle Fabaceae, bottom Poaceae. Species richness on x-axis, and mean disease incidence for each species on y-axis. Lines represent best fit for each species using linear model.

Family Richness Dilution

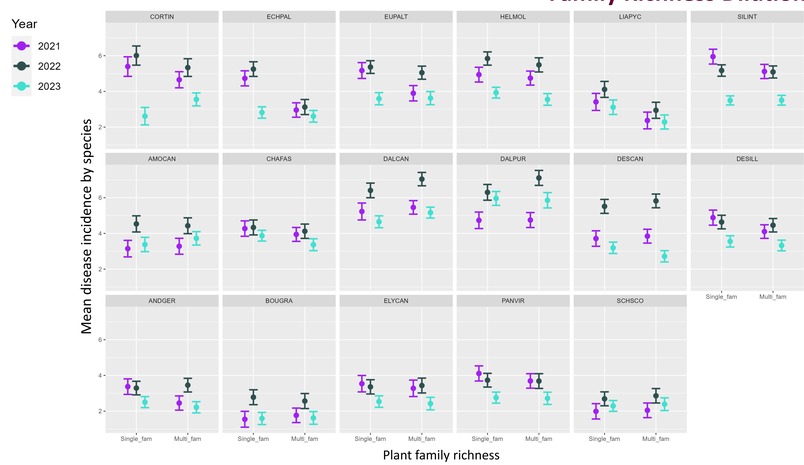


Figure 4 – **Foliar disease dilution in plant family mixtures.** Top row Asteraceae, middle Fabaceae, bottom Poaceae. Mean disease incidence on y-axis, plant family dilution on x-axis.

Pathogen Release Drives Complementarity

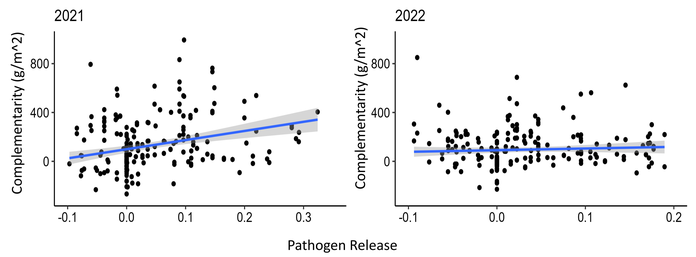


Figure 5 – **Pathogen release predicting complementarity.** Complementarity in 2021 had a strong positive response to predicted pathogen release (left, p=0.0009), while there was no relationship found in 2022 (right, p=0.3). We have not calculated 2023 complementarity yet, but plan to test for this response again.

Table 1 – **Mixed model.** Disease incidence response by species, species and plant family, and precipitation treatments. On the left, species as a fixed effect and on the right, species as random to measure overall treatment response across species-specific variation

Full Model Type III ANOVA	*Species fixed effect*		*Species random effect*	
	F-val	Pr(>F)	F-val	Pr(>F)
Subblock	0.733	0.63	0.65	0.67
Year	200.16	**<2.2e-16**	203.75	**<2.2e-16**
Species	39.95	**<2.2e-16**		
SpRich	17.94	**3.99E-05**	9.38	**0.003**
Phylo	9.45	**0.002**	4.63	**0.03**
Precip	0.25	0.62	0.21	0.65
SpRich*Phylo	2.03	0.16	0.7	0.4
SpRich*Precip	0.5	0.48	0.46	0.5
Phylo*Precip	1.42	0.23	1.32	0.25
Species*SpRich	4.33	**1.79E-08**		
Species*Phylo	5.51	**1.01E-11**		
Species*Precip	1.97	**1.20E-02**		

Conclusions

Our results demonstrate **foliar pathogen dilution with increased plant species, as well as plant family, richness**. When tested across the variation between plant species, we found that pathogen dilution due to both species and family richness is consistent across variation among plant species. Together, this suggests that **foliar pathogen dilution is common, and particularly strong with inclusion of phylogenetically diverse plant species pools**, affirming expectations associated with patterns driven by plant pathogen specificity (Gilbert & Webb 2007). This finding indicates that one reason for the mixed findings in previous tests of foliar pathogen dilution could be due to inconsistency in phylogenetic diversity of the species pool which are used in the experiment. Pathogen dilution was consistent across precipitation treatments, with **no consistent effect of precipitation on foliar disease incidence or dilution**. Finally, as productivity increased with predicted release from foliar pathogens, we provide **direct evidence that dilution of foliar pathogens can have consequences for terrestrial function**. Together, this work highlights the generality and significance of pathogen dilution in plant communities and terrestrial function.

Cited work. Gilbert, Webb. Phylogenetic signal in plant pathogen-host range. *Proceedings of the National Academy of Sciences* **104**, 4979–4983 (2007); Keesing, Ostfeld. Dilution effects in disease ecology. *Ecology Letters* **24**, 2490–2505 (2021); Scholthof. The disease triangle: pathogens, the environment and society. *Nat Rev Microbiol* **5**, 152–156 (2007); Whitaker, Bauer, Bever, Clay. Negative plant-phyllosphere feedbacks in native Asteraceae hosts – a novel extension of the plant-soil feedback framework. *Ecology Letters* **20**, 1064–1073 (2017); Wang, *et al.* Soil microbiome mediates positive plant diversity-productivity relationships in late successional grassland species. *Ecology Letters* **22**, 1221–1232 (2019); Schnitzer, *et al.* Soil microbes drive the classic plant diversity–productivity pattern. *Ecology* **92**, 296–303 (2011); Maron, Marler, Klironomos, Cleveland. Soil fungal pathogens and the relationship between plant diversity and productivity. *Ecology Letters* **14**, 36–41 (2011); Bever, Mangan, Alexander, Maintenance of Plant Species Diversity by Pathogens. *Annu. Rev. Ecol. Evol. Syst.* **46**, 305–325 (2015); Hector, Beale, Minns, Otway, Lawton. Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. *Oikos* **90**, 357–371 (2000).

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