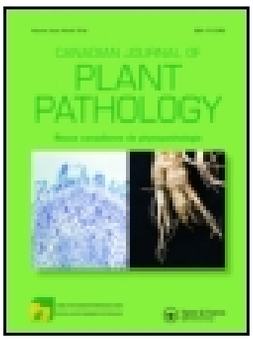

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Structure and diversity of *Fusarium* communities inhabiting non-cultivated grass inflorescences in New York State

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Abstract: The structure and diversity of wild grass spike-inhabiting *Fusarium* communities are not well understood. Fifteen common, non-cultivated grasses were surveyed across two years, regions, and land uses for spike-dwelling *Fusarium* spp. Eleven fungal species were identified from 857 isolates, including two, *F. camptoceras* and *F. lactis*, not recorded previously in New York state or on grass hosts. Species diversity and community structure varied by year and region. Land use and host community did not influence *Fusarium* communities, and no species-specific grass-*Fusarium* associations were detected. *Fusarium* communities were divided into two categories, those dominated by *F. graminearum* and those dominated by *F. sporotrichioides*. The community formation process is relevant to disease prediction and toxin monitoring in cropping systems as well as to land management practices at the intersection of agricultural and natural spaces.

Keywords: community ecology, fungal diversity, *Fusarium*, wild grasses

Résumé: La structure et la diversité des communautés de *Fusarium* qui colonisent les épis de graminées sauvages ne sont pas bien comprises. Quinze espèces de graminées sauvages courantes ont été étudiées pendant deux ans dans diverses régions et sur des terres affectées à différentes utilizations afin d'y détecter des espèces de *Fusarium* qui colonisent leurs épis. Onze espèces fongiques ont été identifiées à partir de 857 isolats, y compris deux, *F. camptoceras* et *F. lactis*, à ce jour jamais trouvées dans l'État de New York ou sur des graminées hôtes. La diversité des espèces et la structure des communautés variaient en fonction des années et des régions. L'utilization des terres et la communauté d'hôtes n'ont pas influencé les communautés de *Fusarium*, et aucune association spécifique graminées-*Fusarium* n'a été détectée. Les communautés de *Fusarium* ont été divisées en deux catégories: celles dominées par *F. graminearum* et celles dominées par *F. sporotrichioides*. Le processus de formation des communautés est déterminant pour la prédiction des maladies et le suivi des toxines dans les cultures ainsi que pour la gestion des terres situées à la jonction de l'espace agricole et de l'espace naturel.

Mots clés: Diversité fongique, Écologie des communautés, *Fusarium*, graminées sauvages

Introduction

Fusarium is a cosmopolitan genus containing many plant pathogen species with significant economic impacts (Booth 1971). A number of *Fusarium* spp. have wide host ranges that include non-cultivated grasses (Farr and Rossman 2019). While previous surveys have recorded the incidence of various *Fusarium* spp. in wild grasses (Inch and Gilbert 2003; Turkington et al. 2011; Szécsi et al. 2013; Lofgren et al. 2017) none have explicitly considered the influence of different environments or host plants on community composition. Because these fungal pathogens often damage staple crops, like wheat and maize, and contaminate grain with diverse mycotoxins (Marasas et al. 1984), the factors driving species diversity and structuring communities have relevance to disease prediction and monitoring in agricultural systems. Grasses growing in close proximity to crops may serve as pathogen reservoirs, contributing disease-inciting propagules and providing opportunities for survival between cropping cycles. Understanding the

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ecology of multi-host pathogens may also lead to land management practices that benefit natural host plants where agricultural and non-agricultural environments meet. The spillover of plant pathogens from one host to another can result in changes in host species abundance (Power and Mitchell 2004). Multiple grass inhabiting fusaria are capable of causing seedling blights and root rots in crops, and if *Fusarium* communities change as a result of proximity to agricultural production there may be an impact on natural host communities. Understanding grass-*Fusarium* community dynamics requires an understanding of the drivers of species diversity and community structure. In particular, the role of the environment and of the host community in shaping wild grass spike-inhabiting *Fusarium* communities are of interest because both are known to be important in agricultural contexts (Zhang et al. 2016; Bankina et al. 2017; Yang et al. 2018).

In this study, we leveraged the presence of diverse host communities found across New York State to: (i) compare *Fusarium* species diversity between regional and local environments; (ii) identify factors structuring these communities; (iii) and relate host communities to pathogen communities. Species diversity was expected to be highest in diverse plant communities remote from agricultural production, while proximity to agricultural production was expected to cause a decrease in species diversity and changes to community structure.

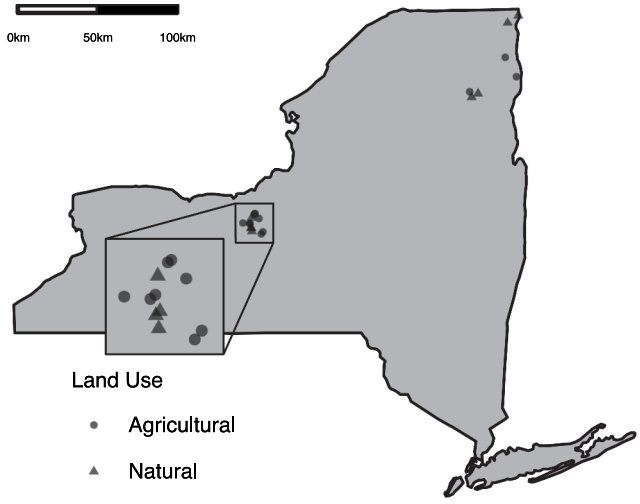

Fig. 1 Grass inflorescences were sampled from 19 locations over 2 years. Field sites were divided between two regions of New York State and two land-use categories: agricultural and natural.

Table 1. Sampling depth over years, regions and land uses.

Year	Region	Land Use	Spikes Sampled	Fusarium Isolates
2016	Central	Agricultural	695	67
		Natural	495	46
2017	Central	Agricultural	576	251
		Natural	410	176
	Northeastern	Agricultural	780	247
		Natural	338	70

Materials and methods

Fungal cultures and species identification

The isolates used in this study were recovered in the course of a field survey recording *Fusarium graminearum* incidence in wild grasses (Fulcher et al. 2020). Briefly, non-cultivated grass spikes were collected in June 2016 and 2017 from 19 field sites in New York State (Fig. 1). Sampling was performed in two regions, Central and Northeastern New York, which differed in host density and level of agricultural production. Within each region, both agricultural fields and non-managed, natural spaces were sampled (Table 1). Only the Central region was sampled in 2016, while both regions were sampled in 2017. Plant tissue was taken from 1 m^2 quadrats laid on transects following the margins of crop fields or along transects placed randomly in natural grass communities. Grass species richness was also recorded in quadrats at the time of sampling. The quadrats were separated by 10 m, and sites were no closer than 1 km from one another.

Fusarium spp. colonies were recovered from surface-sterilized host tissue, and only a single fungal culture was saved from each grass spike. Single-spore derived isolates were stored as conidial suspensions at −80°C until further use. *Fusarium graminearum* was identified morphologically (Leslie and Summerell 2006). Taxonomic placement was confirmed for a subsample of these isolates using the molecular methods detailed below. All non-*graminearum* isolates were grown on potato dextrose agar for one week under 12-hr fluorescent light cycles at room temperature. Mycelia were scraped from the agar's surface and placed into 2 mL microcentrifuge tubes with 1 g of garnet beads. Tubes were frozen at −20°C and tissue was ground using a Vortex-Genie 2 (Scientific Industries, Bohemia, NY, USA). DNA extraction proceeded using a commercial kit according to manufacturer instructions (DNeasy Plant Mini Kit, QIAGEN, Hilden, Germany). Taxonomic placement of isolates was based on partial sequences of

either the translation elongation factor 1-alpha (*TEF-1α*) or RNA polymerase II subunit (*RPB2*) genes (Ward et al. 2002; O'Donnell et al. 2015; Lofgren et al. 2017). While a fragment of either gene is able to resolve *Fusarium* to the species complex level, the *RPB2* locus was used for the majority of samples because PCR amplification was more consistent. Amplified DNA was visualized with gel electrophoresis, cleaned with a commercial silica spin column kit (QIAquick PCR Purification Kit, QIAGEN, Hilden, Germany; Monarch PCR & DNA Cleanup Kit, New England Biolabs, Ipswich, MA, USA), and submitted to the Cornell Biotechnology Resource Centre for sanger sequencing (ABI 3730xl, Applied Biosystems, Foster City, CA, USA). Sequences were managed in Geneious Prime version 2019.0.4 (Biomatters, Auckland, New Zealand), trimmed for quality, and compared to those from known specimens deposited in curated culture collections (e.g. CBS or NRRL) and type cultures accessioned in NCBI Genbank using BLAST (Altschul et al. 1990). Species or species complex identification was considered positive when sequence homology was ≥ 98% to a single taxonomic assignment.

Statistical analyses

All statistical analyses were performed in RStudio version 1.1.453 (RStudio Development Team, 2016). Individual *Fusarium* species incidence was analysed with a multinomial regression model using the 'nnet' package (Venables and Ripley 2002). A full model was built using year, region, land use, site, and grass host as predictors. Automated, stepwise model selection was performed to minimize Akaike information criterion (AIC) (Hastie and Pregibon 1992; Venables and Ripley 2002). The final model, with the lowest AIC, was subjected to analysis of variance to identify the variables that most effectively explained the data, and these were included in further analyses. The probability of each species occurring given region and land use was estimated with 95% confidence intervals using the 'emmeans' package (Lenth 2019).

Alpha diversity of *Fusarium* spp. was measured using Hill numbers, or effective species numbers (Gotelli et al. 2014). Rarefaction and estimation of effective species numbers (Hill numbers) at orders 0, 1, and 2 was performed using the 'iNEXT' package (Hsieh et al. 2016). Following Shapiro-Wilk tests for normal distributions (Royston 1992), mean *Fusarium* species numbers were contrasted between years, regions, and land uses with linear models and analysis of variance. Beta diversity was measured and analysed using the 'vegan' package (Oksanen et al. 2018). Community dissimilarity, using Bray-Curtis distances, was contrasted by year, region, and land use with a permutational multivariate analysis of variance. Dispersion within each group was assessed with analysis of variance to ensure any PERMANOVA significance was the result of differences in mean not dispersion (Anderson 2006). Community dissimilarity was also visualized in nonmetric multi-dimensional scaling plots using k = 2 dimensions.

Fusarium community structure was described with a principle components analysis of species abundance data and a Mantel test (using 10 000 random permutations) comparing community distance and physical distance matrices. The diversity and structure of grass communities were also examined using the above methods. The relationship between grass and *Fusarium* species was assessed by correlating their effective species numbers with a linear model and their community dissimilarities with a partial-Mantel test accounting for spatial autocorrelation. Preferential associations between grasses and *Fusarium* species were assessed with a permutation test using 10 000 simulations to generate a X^2 null distribution.

Results

Species identification

There were 51 samples discarded after DNA extraction, PCR amplification or sequencing failed. In total, 857 *Fusarium* isolates were identified as belonging to 11 species (Table 2). Partial gene sequences were deposited to NCBI GenBank (Accession nos.: MN013432-MN013439; MN183343-MN183753). Year (X^2 = *167,* $P < 0.001$), region (X^2 = *240,* $P < 0.001$), and land use (X^2 = *29,* $P = 0.001$) were retained in a multinomial model of species incidence with $\rho^2 = 0.180$, indicating a good model fit (McFadden 1977). Sample site and grass host identity were discarded during the model selection step because they lacked power to explain *Fusarium* species occurrence. The differences in the probability of each species occurring in grass spikes given region and land use is shown in Fig. 2.

Alpha and beta diversity of Fusarium communities

Effective species number (qD) for order 0 ranged from 1.34 to 3.00, with a mean of 2.12. Increasing to orders 1 and 2 resulted in slightly lower estimates of qD (Fig. 3). Effective species' numbers were assumed normal following Shapiro-Wilk tests ($P \geq 0.307$). Year ($F_{1,18} \geq 6.092$, $P \leq 0.026$) and region ($F_{1,18} \geq 11.499$, $P \leq 0.004$), but not land use ($F_{1,18}$

Table 2. *Fusarium* isolates recovered from grass species.

Species	*acuminatum*	*avenaceum*	*camptoceras*	FGSC[a]	FIESC[b]	*lactis*	*poae*	*proliferatum*	*sambucinum*	*sporotrichioides*	*subglutinans*
Alopecurus arundinaceus	1	–	–	–	–	–	–	–	–	–	–
Brachypodium sylvaticum	–	–	–	1	–	–	–	–	–	–	–
Bromus commutatus	–	–	–	14	1	–	–	–	–	4	–
Bromus inermis	2	2	1	41	4	–	2	–	1	65	–
Bromus secalinus	–	–	–	1	1	–	–	–	–	–	–
Dactylis glomerata	2	6	–	160	4	–	2	–	–	58	–
Elymus repens	1	4	–	62	2	–	11	2	–	31	1
Festuca spp.	2	3	–	43	6	–	3	–	–	31	–
Hordeum jubatum	–	1	–	–	–	–	1	–	–	1	–
Lolium perenne	–	–	–	–	–	–	2	–	–	1	–
Panicum spp.	–	1	–	3	–	–	–	–	–	1	–
Phalaris arundinacea	–	1	–	81	1	1	8	–	–	42	–
Phleum pratense	–	5	–	37	9	–	11	–	–	39	–
Poa annua	–	2	–	15	3	–	1	–	–	14	–
Typha latifolia	–	–	–	–	–	–	–	–	–	1	–

[a]*Fusarium graminearum* species complex (FGSC) or *Fusarium graminearum* sensu lato
[b]*Fusarium incarnatum-equiseti* species complex (FIESC)

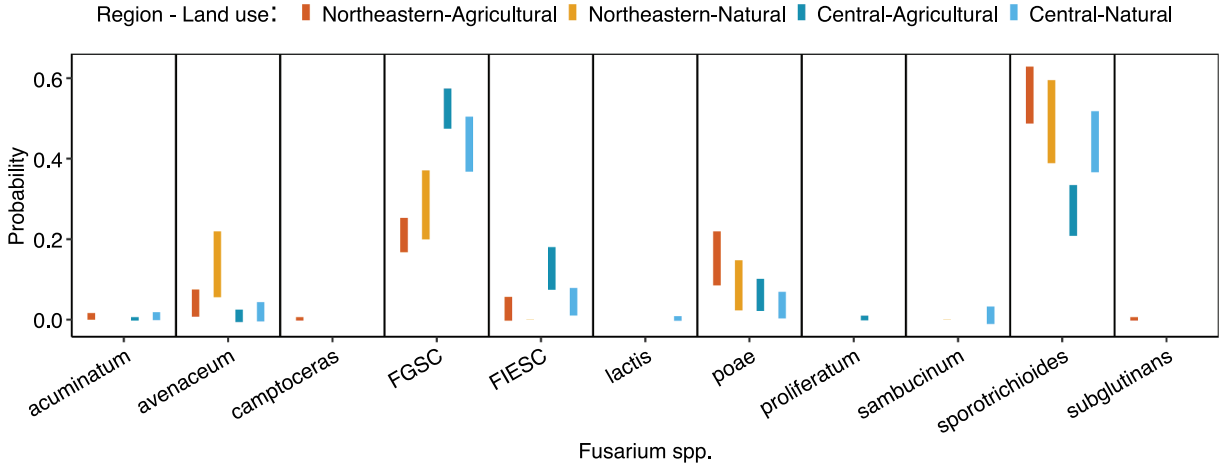

Fig. 2 The probability of a given *Fusarium* species occuring in a region and land use. Bars represent 95% confidence intervals from multinomial logistic regression estimates.

≤ 2.397, $P \geq 0.142$), had significant effects on effective species number at all three orders (R^2 = 0.400–0.441). Natural sites in Northeastern New York had the highest species diversity, while agricultural sites in Central New York had the lowest. Community dissimilarity was associated with differences between year ($R^2 = 0.167$, $F_{1,18} = 4.200$, $P = 0.004$) and region ($R^2 = 0.182$, $F_{1,18} = 4.575$, $P = 0.003$), but not land use ($R^2 = 0.540$, $F_{1,18} = 1.368$, $P = 0.236$) according to PERMANOVA. Dispersion around group means did not vary for year ($P = 0.415$), region ($P = 0.884$) or land use ($P = 0.180$). An nMDS plot shows moderate differentiation for year and region (Fig. 4).

Fusarium community structure

The principle components analysis showed nearly all variation in *Fusarium* populations was attributed to the relative abundance of *F. graminearum* and *sporotrichioides*, the two most frequently recovered species (Fig. 5). The communities found in Central New York during 2016 grouped together with the communities found in Northeastern New York during 2017. No spatial correlation in community dissimilarity was detected with a Mantel test (r = 0.106, $P = 0.117$).

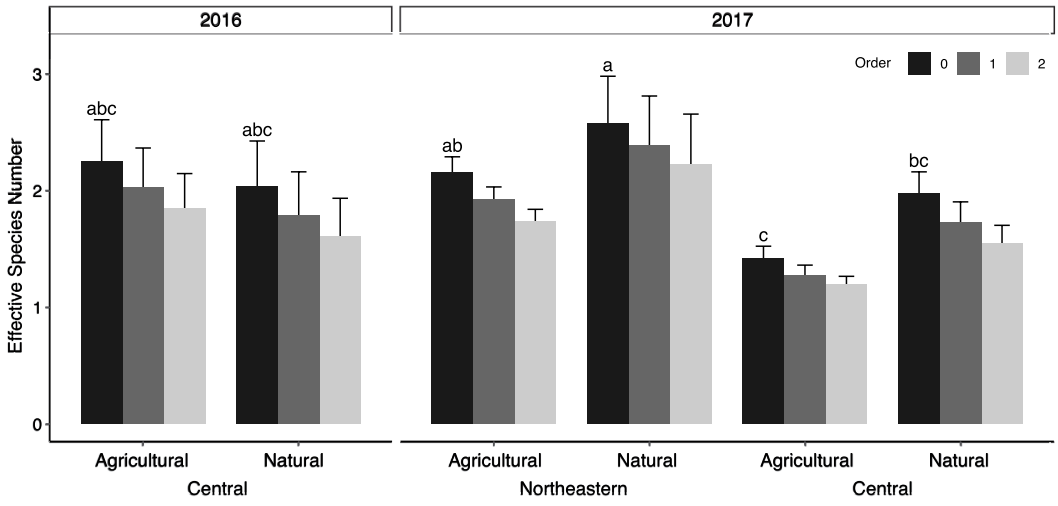

Fig. 3 Effective species, or Hill numbers (qD), were obtained by rarifying species abundance and compared across year, region, and land use. *Fusarium* species diversity differed significantly between years and regions but not between land uses. Filled bars represent mean values and error bars indicate standard deviation. Pairwise comparisons were conducted to identify differences in mean effective species number at each order of q, and Tukey's Honest significant differences were calculated at alpha = 0.05. Bars of the same shade with the same letter were not significantly different.

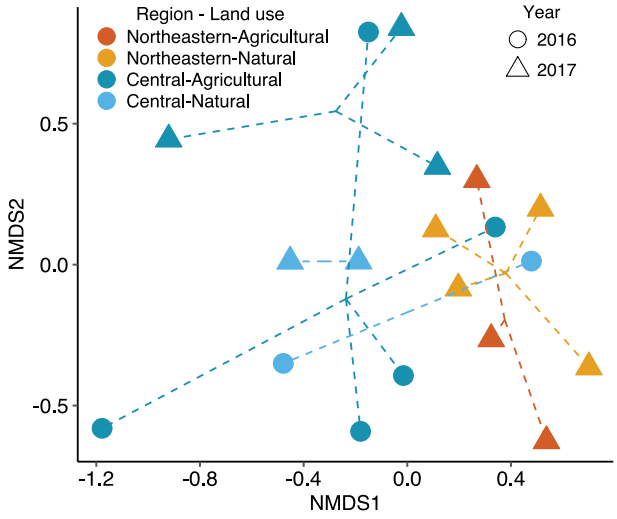

Fig. 4 Community dissimilarity visualized with a non-metric multidimensional scaling plot (Stress = 0.141). According to a PERMANOVA of Bray-Curtis dissimilarities, the effect of year and region were significant.

Relating Fusarium and grass communities

The effective species estimates for grass and *Fusarium* communities were not correlated (r = −0.13, P = 0.599 for qD of order 0). Community dissimilarity was not correlated according to a partial Mantel test (r = 0.56, P = 0.281). The X^2 test failed to find differential association between *Fusarium* species and grass species (P = 0.061).

Discussion

This is the first study to catalogue *Fusarium* species diversity in non-cultivated grasses in New York, including those found in the Adirondack Mountains' wilderness and a 4,000 hectare national wildlife refuge. The geographic or host ranges of several uncommon *Fusarium* spp. were expanded by this study. Our findings also show communities are likely structured by annual and regional factors, rather than the local environment or host community. This contrasts with findings for soil-borne *Fusarium* communities, which vary significantly between hosts (LeBlanc et al. 2017), and does not support our hypothesis of positive correlation between fungal pathogen diversity and grass diversity, which has been shown for foliar fungal pathogens (Rottstock et al. 2014). Our results may help predict pathogen population diversity and, by extension, toxin potential in different environments, specifically those with varying levels of rainfall and host density, which is potentially useful for monitoring disease and toxin content in crops. The findings also suggest altered land management practices at the intersection of crop and natural host communities, like adding buffer strips or restricting crop production, would have little influence on pathogen populations in nearby grasses.

The most common *Fusarium* species, such as *F. graminearum* and *sporotrichioides*, were well distributed across hosts, evidenced by a lack of any particular

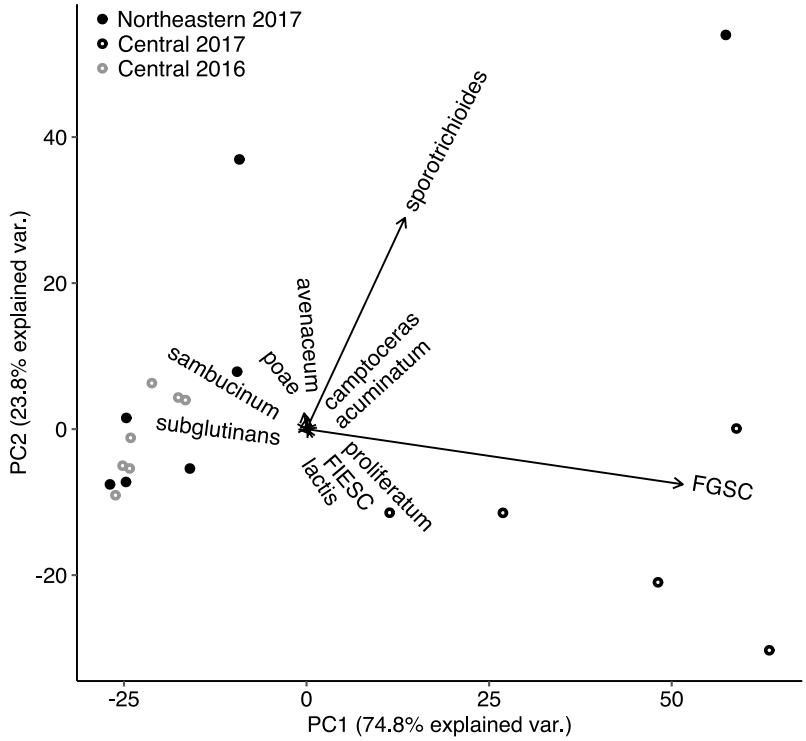

Fig. 5 Principal components analysis of *Fusarium* species abundance at 19 sites. Community differences were attributable to large variation in the occurrence of two *Fusarium* species, *sporotrichioides* and *graminearum*. Central New York sites in 2016 experienced a drought, which led to communities more similar to those in low host density Northeastern New York during 2017 than to nearby communities in 2017 during a year of average rainfall.

host-*Fusarium* associations. Most of the *Fusarium* species recorded here have previously been reported from numerous hosts, particularly plants in the true grass family, Poaceae (Farr and Rossman 2019). Culture-based approaches to fungal community surveys are limited in their depth and are likely to underestimate diversity. The results are inherently biased towards the most abundant species and species with high growth rates under the conditions imposed by isolation. However, even with the current approach, saving only a single isolate from each plant sample, singleton isolates were recovered that represent the first instances of certain species occurring in New York State or in association with a grass host. *Fusarium camptoceras* is most often found in association with rotting tropical fruits (Li-Sha et al. 2013; Abd Murad et al. 2017), but was once recorded from shattered wild rice (*Zizania palustris*) in Minnesota (Nyvall et al. 1999). This is the first recorded occurrence in New York and from smooth brome (*Bromus inermis*). *Fusarium lactis* causes internal fruit rots in sweet pepper and fig (Ploetz 2003; Van Poucke et al. 2012). This isolate is the first from any grass host (*Phalaris arundinacea*), and the first found in New York State.

Annual and regional environments were more important to *Fusarium* species diversity than local environments or grass communities. Despite not being informative at the community level, land use explained significant variation in the incidence of individual *Fusarium* spp. according to multinomial regression. The categorization of sites into two land uses, natural and agricultural, captured specific differences of interest related to disturbance and management practices, like residue removal, tillage, and crop rotation, but failed to account for many other differentiating factors. No attempt was made to quantify landscape features including non-host plant ground cover, elevation or land use in the immediate vicinity. It is likely that quantitative differences between field sites environments lead to changes in community that the present approach was unable to detect. Variation expected between year and region, for example rainfall and host density, are clearly important factors and may also vary on a field to field basis. Indeed, work focusing on *F. graminearum* has shown rainfall and host density are able to explain variation in pathogen incidence in grasses (Fulcher et al. 2020), and these factors were already recognized as

driving crop disease epidemics (Leplat et al. 2013; Manstretta et al. 2016). The occurrence of various *Fusarium* species in crop hosts has also been related to regional differences in host community composition (Xu and Nicholson 2009), and the regions sampled in this study did vary in both host density and the ratio of agricultural to non-agricultural hosts. Within *Fusarium* communities, two species were dominant. Alongside *F. graminearum*, a number of less common pathogens or saprophytes were found. Environments more favourable to *F. sporotrichioides* also had a greater incidence of other crop pathogens, like *F. avenaceum* and *poae*. These differences in composition could be linked to individual life-histories. Because *F. graminearum* is homothallic, and the only species observed to reproduce sexually under natural conditions, it is more readily spread via airborne ascospores than other species capable only of producing asexual conidia. Conidia are splash or wind dispersed over short distances, while ascospores are capable of kilometre-scale movement (Paul et al. 2004; Maldonado-Ramirez et al. 2005; Keller et al. 2014).

It was surprising to find no spatial correlation in community dissimilarity matrices after seeing strong differentiation of communities based on regional location. The Mantel test used to assess spatial structure has been the subject of criticism in part because of its low power (Legendre et al. 2015). The Mantel test was unable to account for annual variation, which might mask the spatial variation in a rough analysis but is easily incorporated into linear models.

To summarize, this study recorded significant regional and annual variation in *Fusarium* communities and species diversity that was not influenced by local land use or individual host species. Two distinct communities, corresponding to a high and low incidence of the major agricultural pathogen *F. graminearum*, were detected and contained different species capable of producing distinct mycotoxin cocktails. Understanding when these different communities form will aid crop disease management and toxin monitoring efforts. The potential impact of these different communities on grasses in natural spaces should be further investigated, especially at the level of individual plant-fungus interactions.

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