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Influence of Groundcover Vegetation, Soil Physicochemical Properties, and Irrigation Practices on Soil Fungi in Semi-arid Vineyards

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Although plants are known to have a strong influence on soil biota, the effect of groundcover vegetation in perennial cropping systems on soil fungi has been little explored. We surveyed extensively managed vineyards to determine how plant community functional characteristics, soil factors, and irrigation management related to the abundance of two guilds of soil fungi that may play a role in plant-soil feedback (entomopathogenic fungi represented by *Beauveria bassiana,* and the pathogenic species complex, *Ilyonectria* spp.). We found that plant community characteristics were related to fungal abundance for both fungi assayed. *Beauveria bassiana* increased with native species, annual plants, and legumes consistently across sampling periods. *Ilyonectria* spp. increased with the abundance of forbs and exotic species, though only the relationship with forbs was consistent across sampling periods. Both fungal guilds increased with increasing soil organic matter. The use of dual or sprinkler irrigation systems also increased *B. bassiana* and *Ilyonectria* spp. in vineyard soils. Overall, groundcover vegetation played a significant role in driving abundance of these important groups of soil fungi. Groundcover management may therefore be a viable tool to manipulate soil fungi with the potential for improving ecosystem services such as conservation biological control of soil dwelling insect pests and deterring pathogens in perennial cropping systems.

Keywords: cover crops, entomopathogenic fungi, black foot disease, conservation biocontrol, vineyards

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INTRODUCTION

Perennial agriculture is characterized by crop rows alternating with drive rows to facilitate field and tractor work. This means that much of the land area in a perennial cropping system is not actually planted to crop plants, but subjected to floor management practices. Depending on regional climate patterns, pest pressure, nutrient challenges, and aesthetics, different strategies are used to manage drive rows. Perhaps the most common approach is the maintenance and management of vegetation in the drive row using cover crops or groundcovers that provide a host of ecosystem services, such as improved carbon sequestration, pest control, and soil fertility (Winter, 2018). With increasing interest in the linkage between soil microbial diversity and ecosystem functioning (Bardgett and van der Putten, 2014) and the potential for groundcover vegetation to affect crop plant health

through plant-soil feedbacks (Vukicevich et al., 2018), a logical question is: how does groundcover vegetation affect key groups of soil biota?

Plants alter the spatial distribution of soil resources through rhizodeposition (Badri and Vivanco, 2009) and litter decomposition (Fanin et al., 2014), creating unique nutrient rich patches that vary with plant species (Broeckling et al., 2008; De Deyn et al., 2011). In fact, specific plants have been used by farmers for millennia to affect changes in populations of soil microorganisms, e.g., through crop rotations (Bullock, 1992). Because rotation of the crop plant is not possible in perennial vineyards and orchards, the drive row then provides an opportunity to introduce plant diversity and subsequently soil microbial diversity to the system (Vukicevich et al., 2016). Cover crops or permanent groundcovers could have particularly pronounced effects on important crop pathogens and mutualists as evidenced by the strong effects of plant identity on soil fungi (De Bellis et al., 2007; De Deyn et al., 2011; Corneo et al., 2013; Lankau and Lankau, 2014; Detheridge et al., 2016).

One beneficial group of soil fungi in agriculture is the entomopathogenic (EP) fungi. EP fungi, typified by the well-studied and commercially sold *Beauveria bassiana* and *Metarhizium anisopliae*, are naturally common in soils where they are responsible for regulation of insect pest communities and appreciated as biocontrol agents (Shah and Pell, 2003; Pell et al., 2010). Living in close association with plants (Moonjely et al., 2016), they are even able to transfer N from infected insects to a plant host in return for plant carbon (Behie et al., 2012, 2017). They have also been implicated in plant protection from soilborne disease (Ownley et al., 2010). Because they may show rhizosphere specificity to some degree (Hu and St. Leger, 2002; Behie et al., 2015) and are preferentially associated with certain types of habitats (Meyling et al., 2009), vineyard groundcover management might also affect the abundance of these beneficial fungi thereby promoting positive plant-soil feedback through regulation of soil dwelling insect herbivores and decreases in plant disease.

In addition to beneficial soil fungi, generalist soil borne plant pathogens that harm woody perennial crops may build up on certain alternate host plants. For example, Agustí-Brisach et al. (2011) found *Ilyonectria* spp., the causal agent of black foot disease of grape, living in various asymptomatic common vineyard weeds. Because some groundcover plants may be good hosts for these pathogens, there is potential for spillover onto grapevine roots that occupy the same soil space. The perceived benefit of increased microbial diversity through enhanced vegetative diversity may be negated if these generalist pathogens accumulate in non-crop vegetation and promote establishment of disease in vines. On the other hand, certain groundcover plants have been seen to decrease the prevalence of these fungi and improve replant outcomes in crops such as apple (Manici et al., 2015). The choice of groundcover may therefore contribute to negative plant-soil feedback on vines if it promotes pathogens like *Ilyonectria* spp. or minimize negative feedbacks if it deters these fungi.

Understanding how to manage groundcover vegetation for positive plant-soil feedback via increasing beneficial fungi while deterring pathogenic fungi could improve the sustainability of perennial crop production (Vukicevich et al., 2016). Though some work has shown that vegetation management can increase overall microbial biomass and activity in vineyard soils (Ingels et al., 2005; Whitelaw-Weckert et al., 2007; Steenwerth and Belina, 2008), how groundcovers may change key fungal guilds over time remains largely unknown.

We sampled groundcover plant communities and associated soils from vineyards in the Okanagan valley, British Columbia. This provided a variety of groundcover management practices that already exist in vineyards in this region to test for effects on soil microbes in real world cropping scenarios. Across these vineyards, we studied how groundcover vegetation affects the abundance of the common EP fungus, *B. bassiana*, and plant pathogenic *Ilyonectria* spp. We used a model-selection approach to identify which plant community characteristics, irrigation techniques, and soil physicochemical factors affected the abundance of each of these fungal guilds as measured by digital droplet PCR (ddPCR) assays. Although there are no published studies that look specifically at how plant functional characteristics affect these groups of soil fungi, we made some predictions based on a review of related literature (Vukicevich et al., 2016). Specifically, we predicted that native plants might increase the abundance of EP fungi (Meyling et al., 2009). Legumes in groundcovers might also be expected to increase EP fungi (Shapiro-Ilan et al., 2012). We expected that *Ilyonectria* spp. might accumulate under legumes (Benitez et al., 2016), but might be less abundant with grasses as grasses seem to be less suitable hosts compared to other vineyard floor vegetation (Agustí-Brisach et al., 2011).

METHODS

Field Sites

All five field sites were located in the southern Okanagan Valley (British Columbia, Canada) (from 49°33′52.44″N, 119°38′19.55″W south to 49° 4′44.02″N, 119°30′41.78″W). This region receives on average ∼320 mm of precipitation annually in the form of snow in winter months and occasional rainfall in spring, summer, and fall. We chose vineyard sites that had different vegetation management schemes within the same vineyard block, i.e., alternating rows or randomized complete block designs. Sites were chosen independent of soil type or management practices, which were controlled for statistically. Site characteristics, including groundcover schemes and irrigation types, are given in **Table 1**.

Plant Community Assessment

We quantified plant communities using quadrats measuring 25 × 50 cm. Four quadrats were evenly spaced throughout four rows of each management scheme (in the case of alternating rows at sites BM, MH, and BC) or four replicate plots (in the case of randomized complete block designs at sites PME and PCH) making for 16 quadrats per management scheme at each site at each sampling period. Nearly 800 plant communities and concomitant soil samples were analyzed in total over the course of this study. Details of sample collection at each site

TABLE 1 | Characteristics of vineyard sites sampled during this project.

Site	Location	Soil series	Pest/fertility management	Groundcover types[a]	Irrigation[a]	Year GC established	Dates sampled	# Samples taken each date[b]
PME	Summerland, BC	Osoyoos sandy loam	"Integrated"	Exotic grass mix; Exotic grass mix plus legumes; Native grass mix; Native grass mix plus forbs	Sprinkler Dual Drip Dual	2014	su 2015; sp 2016; su 2016; sp 2017	64
PCH	Summerland, BC	Osoyoos sandy loam	"Integrated"	Exotic grass mix; Buffalo grass; Grass plus legumes; Clean cultivation	Dual	2011	su 2015; sp 2016; su 2016; sp 2017	60
BM	Okanagan Falls, BC	Rutland sandy loam	"Organic"	Sheep fescue; Annual mix	Sprinkler	2010; 2015	su 2015; sp 2016	32
MH	Oliver, BC	Ratnip sandy loam	"Organic"	Pollinator mix; Resident vegetation	Dual; drip	2009	su 2015; sp 2016; su 2016; sp 2017	32
BC	Osoyoos, BC	Osoyoos sandy loam	"Integrated"	Fescue mix; Alfalfa + perennial ryegrass; Yarrow	Sprinkler	2009	su 2016; sp 2017	64

Inherent differences among sites were controlled for statistically by the inclusion of site as a random factor in the mixed models.

[a] *If more than one irrigation type in place at a site, irrigation type is listed in corresponding order to groundcover type with which it is coupled, except for MH, which transitioned from dual to drip between summer 2016 and spring 2017.*

[b] *Equal numbers of samples were taken from each ground cover type at each site and situated in a consistent spatial pattern (e.g., four alternating vineyard rows with four samples per row with each sample occurring every 10 m). Sample location was accounted for in the mixed model.*

are given in **Supplementary Materials**. Vines adjacent to quadrat placement were marked to facilitate sample collection from the same location at each sampling event. Visual estimation of percent coverage of the quadrat by each plant species was used as a proxy for relative abundance.

Soil Collection and Processing

We collected three soil cores (2.5 × 20 cm) per quadrat, pooled them in sealed plastic bags and kept them on ice for transport to a −20°C freezer. Samples were then weighed, oven dried at 60°C for 72 h to ensure DNA extraction from equal quantities of soil in each sample, and sieved to 2 mm to remove most roots and rocks and homogenize samples. Dried samples were stored at −20°C until use.

Soil Physicochemical Factors

As soil abiotic factors may also be important determinants of fungal abundance in soils, a composite sample of post-processed (after drying and sieving) soil for each treatment was sent to Zenalytic Laboratories (Kelowna, BC) for analysis of organic matter (by loss on ignition) (Davies, 1974), Total N (Kjeldahl, 1883), Extractable P (Mehlich-3 ICP)(Mehlich, 1984), and pH (1:1 in water) (Jackson, 1956).

Molecular Analysis

A 0.5 g subsample was then taken for DNA extraction and quantification of fungi. Genomic DNA was extracted from bulk soil using the FastPrep spin kit for soils (MP Biomedical, Carlsbad, CA) following the manufacturer's instructions. Quantification of target fungal groups was then performed using digital droplet PCR (ddPCR). Each protocol was optimized through the use of dilution series and melt curve analysis in qPCR and annealing/extension temperature gradients with both positive pure culture controls and positive environmental samples in ddPCR.

To quantify the EP fungus we used the primer set BB.fw/BB.rv (Landa et al., 2013), which targets *B. bassiana* at the species level. The following was used in a 20 μL final reaction volume: 10 μL QX200 ddPCR EvaGreen supermix (BioRad, Livermore, CA), 250 nM each primer, 2 μL DNA template, and 7 μL nuclease-free water. Droplets were prepared using BioRad droplet generation cartridges and a QX100 droplet generator. Reaction conditions consisted of initial denaturing at 95°C for 10 min followed by 40 cycles of denaturing at 95°C for 30 s, annealing/extension at 56°C for 2 min, 4°C for 5 min, and 90°C for 5 min. To quantify the plant pathogenic *Ilyonectria* spp. we used the primer set YT2F (Tewoldemedhin et al., 2011) and CYLR (Dubrovsky and Fabritius, 2007), which targets *Ilyonectria* spp. (species complex) that cause black foot disease of grape. This primer set has been used to evaluate abundance of *Ilyonectria* spp. (including *I. macrodidyma* and *I. liriodendri*) in nursery soils (Agusti-Brisach et al., 2014) as well as *I. macrodidyma, I. pauciseptatum, Cylindrocarpon destructans,* and *I. liriodendri* in diseased apple roots (Tewoldemedhin et al., 2011). PCR trials using this primer set in our lab also indicate positive amplification for *I. torresensis, I. europaea, I. ianthothele, I. gamsii, Dactylonectria pauciseptum*, *Clyindrocarpon cylindroides,* and *C. olidum,* all of which are known to cause black foot disease of grape (Úrbez-Torres et al.,

2015). The same recipe and reaction conditions were used as described above except for the annealing/extension step was 60°C for 1 min.

After PCR, droplets were read for fluorescence in a QX200 droplet reader (BioRad, Livermore, CA). Only samples with >10,000 droplets were used for analysis. Raw amplitude and cluster data was exported from Quantasoft version 1.7 (BioRad, Livermore, CA) and the open source software "ddPCRquant" (Trypsteen et al., 2015) was used to determine amplicon concentration of each sample.

Data generated during this project can be viewed on the Open Science Framework, following this link: https://osf.io/cxesk/?view_only=f513573264b141389af7cf23e67200b0.

Data Analysis

Quantification of Plant Community Characteristics

To assess the effect of groundcover vegetation on abundance of our two fungal guilds, we first calculated the abundance and species richness of the plant community, as well as the abundance of different functional traits within the community. Plant abundance was calculated as the total % cover of all vascular plants, whereas species richness was the sum of the number of species. For functional traits, we focused on life history strategy (annual, annual/biennial, biennial, biennial/perennial, and perennial), origin (native/exotic), mycorrhizal status (±) and plant functional group (grass, forb, or legume). For the life history strategies, we coded the different strategies ordinally by increasing length (1 = annual, 2 = annual/biennial, etc.), and calculated the community weighted mean using the R package "FD" (Laliberté and Legendre, 2010). We also coded origin and mycorrhizal status ordinally (0 = native, 1 = exotic, and 0 = non-mycorrhizal, 1 = mycorrhizal) and calculated community weighted means, resulting in indices representing the weighted abundance of exotic and mycorrhizal plants within each quadrat. Exotic plants included both seeded exotic groundcover species as well as exotic weedy species. For plant functional groups, we did not recode the groups as there was no obvious order among them. Instead, we calculated the community weighted mean of % cover of each category; however, forb abundance was not used in subsequent models to avoid extreme collinearity among the indicators.

Determination of Effects Using Model Selection

To determine which factors affect the abundance of fungal taxa, we used mixed models in the R package lme4 (Bates et al., 2015) along with model selection. We used separate mixed models for each fungal group (*B. bassiana,* and *Ilyonectria* spp.). Within the mixed models, we included irrigation type, soil characteristics (phosphorus, pH, and organic matter) and plant community characteristics (total cover, species richness, plant life history strategy, mycorrhizal status, origin, and functional groups) as fixed effects. Given that microbial abundance was quantified in multiple seasons and years, we also included interaction terms between each of these predictors and the sampling period. As random effects, we included block nested within site and quadrat nested within block to account for spatial structuring of samples and inherent site differences.

To reduce the complexity of these models, we used a combination of model and variable selection. First, we ran all possible combinations of the models using the *dredge* function in the R package MuMIn (Barton, 2017). These models were then ranked by their AICc score relative to the most parsimonious model (ΔAICc). Models with a ΔAICc score > 2 were considered uninformative and not considered further (Burnham and Anderson, 2002). Using this subset of models, we weighted each variable using the sums of the ΔAICc scores for the models in which they were included using the *model.avg* function in "MuMIn." Variables with a weight > 0.7 were considered important and included in the final model. This procedure was repeated separately for each microbial group. Outputs from the *model.avg* function listing the average importance of all variables tested across all models run using the *dredge* function are given in **Tables S1**, **S2**. For the final models, we also estimated R^2 values, partitioned between the fixed effects and fixed plus random (Nakagawa and Schielzeth, 2013), as implemented in MuMIn.

To aid the interpretation of the effects of sampling periods, we calculated the estimated marginal means for each sampling period using the R package "emmeans" (Lenth, 2018). Additionally, we used the "emtrends" function within this package to compare the slopes between sampling periods in cases where there were significant interactions with the continuous predictors. To enable comparison among indicators, each indicator variable was scaled to a mean of zero and divided by the standard deviation prior to calculating the trends.

Results are organized into two categories based on the two individual models (*B. bassiana,* and *Ilyonectria* spp.) and then based on three subcategories ("plant effects," "soil effects," and "irrigation and time effects") for ease of interpretation and discussion. Full results for each model can be obtained from the Open Science Framework by following this link: https://osf.io/7qctx/?view_only=e0c567cad4f74a57a81185640b93d62a.

RESULTS

Beauveria bassiana

The final model for *B. bassiana* included sample period, irrigation type, plant life history strategy, exotic species, legumes, grasses, organic matter, and soil P, as well as sampling period interaction terms with irrigation type, grasses, legumes, and soil P (**Table 2**). The fixed effects in this model explained 19% of the variation in *B. bassiana* abundance, while 54% of the variation was explained by fixed plus random effects (vineyard site and spatial structuring of sampling). Sampling period affected the abundance of *B. bassiana* [$F_{(3,717)} = 21.93$, $P < 0.001$], with abundance increasing in spring 2017 compared to spring 2016.

Plant Effects on *Beauveria bassiana*

The abundance of *B. bassiana* was consistently related to plant life history strategy, proportion of exotic species, and legumes (**Table 2**). *B. bassiana* decreased with average plant lifespan [$F_{(1,586)} = 3.91$, $P = 0.048$], increased with the proportion of native plant species [$F_{(1,670)}$=11.57, $P < 0.001$], and increased with legume cover [$F_{(1,667)} = 4.84$, $P = 0.03$] (**Figure 1A**). These plant effects were consistent across the experiment, i.e., did not

TABLE 2 | Effect of sampling date and biotic and abiotic factors in the model of *Beauveria bassiana* abundance as tested using Satterwaite type III approximation for degrees of freedom (Model AIC: 2,166, $R^2_{fixed} = 0.19$).

Category	Factor	*F*-value	*P*-value
Time	Sample period[a]	21.93	**<0.001**
Abiotic factors	Irrigation type[b]	7.5333	**<0.001**
	Organic matter	9.70	**0.002**
	Soil P	0.01	0.90
Biotic factors	Exotics[c]	11.57	**<0.001**
	Legumes[c]	4.84	**0.028**
	Grasses	0.18	0.67
	Life history strategy[d]	3.91	**0.048**
Interactions	Sample period × Irrigation type	8.01	**<0.001**
	Sample period × Soil P	3.49	**0.015**
	Sample period × Grasses	8.50	**<0.001**
	Sample period × Legumes	2.51	0.058

Significant ($P < 0.05$) P-values are in bold.

[a] *"Sample period" indicates when the samples were collected (summer 2015, spring 2016, summer 2016, and spring 2017).*

[b] *"Irrigation type" includes drip (no supplemental irrigation applied to groundcover), dual (occasional watering of groundcover), and sprinkler (frequent watering of groundcover when vines are irrigated).*

[c] *"Exotics" and "Legumes" refers to % quadrat covered by: exotic (non-native) species and legume species, respectively.*

[d] *Plant "Life history strategy" was dummy coded along a continuum from annual (1) to perennial (5).*

depend on sampling period. The effect of grass cover was not significant overall, but was positively associated with *B. bassiana* abundance in spring of 2017.

Soil and Irrigation Effects on *Beauveria bassiana*

Soil organic matter had a consistently positive effect on *B. bassiana* [$F_{(1,662)} = 9.70$, $P = 0.002$] (**Figure 1B**). Soil P had no effect overall, but depended on sampling period [$F_{(3,733)} = 3.49$, $P = 0.015$] with a positive relationship seen in spring 2017 (**Figure 1B**).

Irrigation type was also related to *B. bassiana* abundance with dual and sprinkler irrigation increasing *Beauveria* compared with drip irrigation [$F_{(2,689)} = 7.53$, $P < 0.001$], but effects were inconsistent among sampling periods [$F_{(6,719)} = 8.01$, $P < 0.001$] (**Figure 2**).

Ilyonectria spp.

The final model for *Ilyonectria* spp. included sample period, irrigation type, organic matter, soil P, total plant cover, exotic plant cover, and grass cover, as well as interaction terms with sample period for all factors except grass cover and soil P. Fixed effects in this model explained 38% of the variation, with fixed plus random effects explaining 45%. *Ilyonectria* spp. abundance varied with sampling period [$F_{(3,568)} = 12.21$, $P < 0.001$], with a lower amount of *Ilyonectria* spp. detected in spring 2016 compared to the other sampling periods (**Table 3**).

Plant Effects on *Ilyonectria* spp.

The abundance of *Ilyonectria* spp. was consistently negatively associated with grass cover [$F_{(1,531)} = 22.38$, $P < 0.001$]

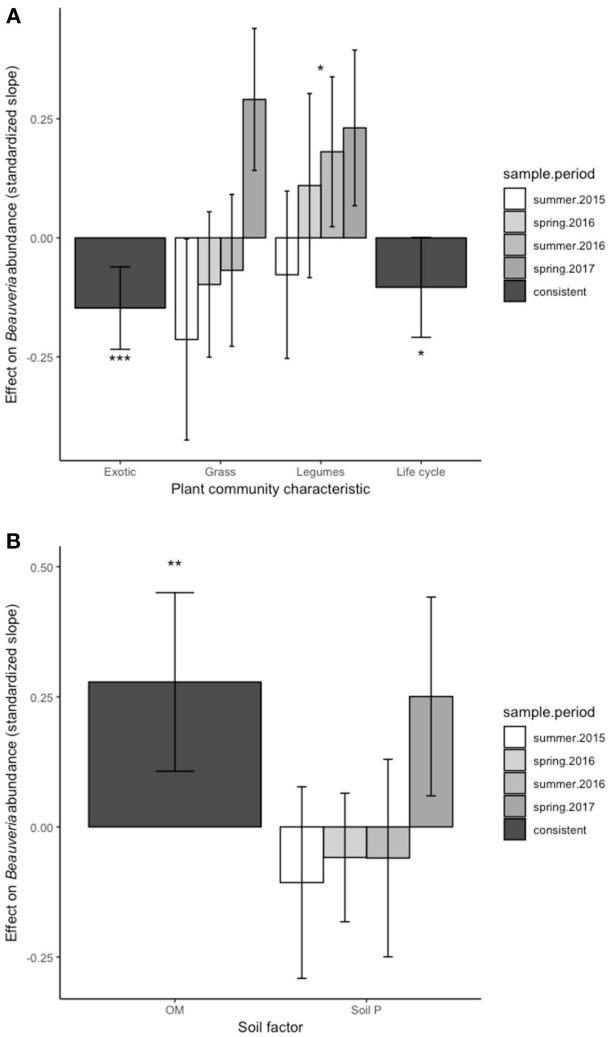

FIGURE 1 | Effect of plant community characteristics **(A)** and soil properties **(B)** on *Beauveria bassisana* abundance. Positive values indicate a positive relationship (standardized slope) between a given factor and *B.bassiana* at that sampling point while negative values represent a negative relationship. A single bar for a given factor means that sampling time did not change the relationship between *B. bassiana* and that factor, i.e., effects were consistent across time. The presence of bars for each sampling time indicates that the relationship between *B. bassiana* and a given factor depended on sampling time. Height of the bar indicates relative strength of each effect. Error bars represent 95% confidence limits. Error bars that do not cross 0 on the y-axis indicate significantly positive or negative relationships between soil factors and *B. bassiana* abundance at a given sample period. "*," "**," and "***" indicate overall significant ($P < 0.05$, 0.01, and 0.001, respectively) positive or negative effects of a factor on *B. bassiana* abundance.

(**Figure 3A**). Overall, *Ilyonectria* spp. increased with exotic plant cover [$F_{(1,675)} = 11.25$, $P < 0.001$], but this relationship varied with sampling period (**Figure 3A**).

Soil and Irrigation Effects on *Ilyonectria* spp.

Soil organic matter was positively related [$F_{(1,47)} = 27.02$, $P < 0.001$] at all sampling periods despite a weak interaction with sampling period [$F_{(3,751)} = 3.06$, $P = 0.03$] (**Figure 3B**).

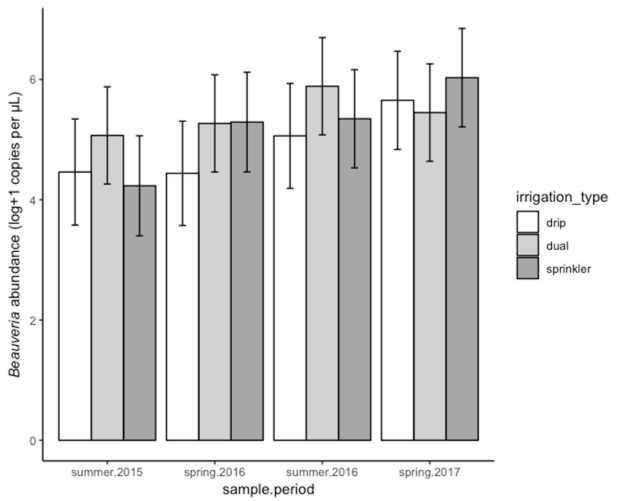

FIGURE 2 | Effect of irrigation type (shades) on *Beauveria bassiana* abundance across all sites at four sampling periods. Error bars indicate 95% confidence limits based on likelihood of these estimates within the final model, i.e., accounting for all other factors included in the model.

TABLE 3 | Effects of sampling date and biotic and abiotic factors in the model of *Ilyonectria* spp. abundance as tested using Satterwaite type III approximation for degrees of freedom (Model AIC: 2,168, $R^2_{fixed} = 0.38$).

Category	Factor	*F*-value	*P*-value
Time	Sample period[a]	12.21	**<0.001**
Abiotic factors	Irrigation type[b]	9.51	**<0.001**
	Organic matter	27.02	**<0.001**
	Soil P	1.77	0.184
Biotic factors	Grasses	22.38	**<0.001**
	Exotics[c]	11.25	**<0.001**
	Total plant cover[c]	3.09	0.079
Interactions	Sample period x Irrigation type	5.02	**<0.001**
	Sample period x Exotics	3.27	**0.021**
	Sample period x Total plant cover	5.14	**0.002**
	Sample period x Organic matter	3.06	**0.027**

Significant ($P < 0.05$) P-values are in bold.

[a] *"Sample period" indicates when the samples were collected (summer 2015, spring 2016, summer 2016, and spring 2017).*

[b] *"Irrigation type" includes drip (no supplemental irrigation applied to groundcover), dual (occasional watering of groundcover), and sprinkler (frequent watering of groundcover when vines are irrigated).*

[c] *"Exotics" and "Total plant cover" refers to % quadrat covered by exotic (non-native) species and all plant species, respectively.*

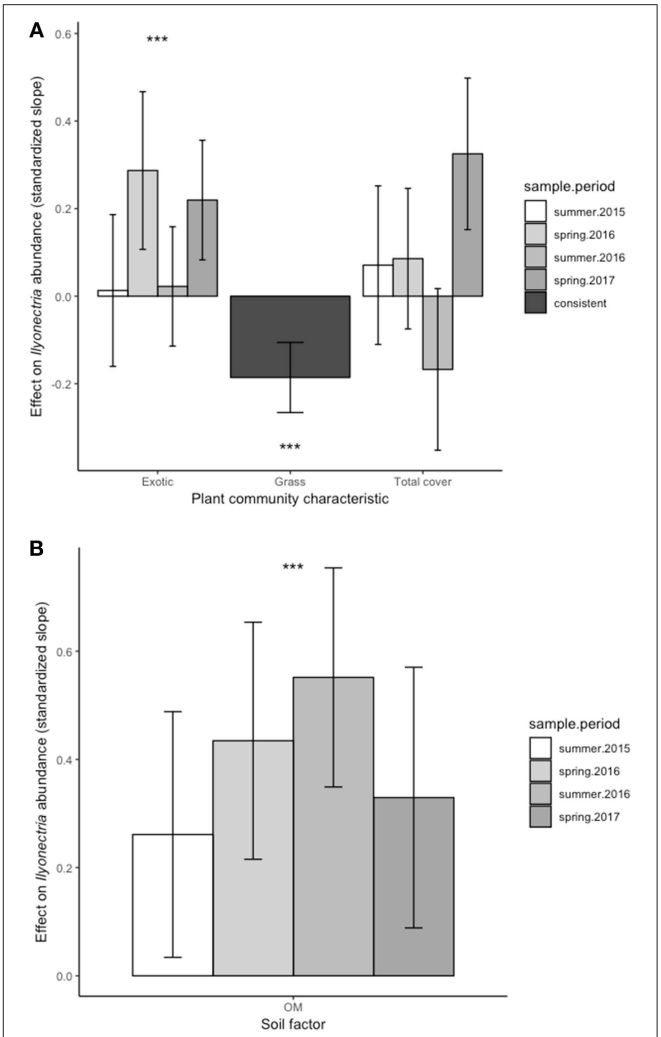

FIGURE 3 | Effect of plant community characteristics **(A)** and soil properties **(B)** on *Ilyonectria* spp. abundance. Positive values indicate a positive relationship (slope) between a given factor and *Ilyonectria* spp. abundance at that sampling point while negative values represent a negative relationship. A single bar for a given factor means that sampling time did not change the relationship between *Ilyonectria* spp. and that factor, i.e., effects were consistent across time. The presence of bars for each sampling time indicates that the relationship between *Ilyonectria* spp. and a given factor depended on sampling time. Height of the bar indicates relative strength of each effect. Error bars represent 95% confidence limits. Error bars that do not cross 0 on the y-axis indicate significantly positive or negative relationships between soil factors and *Ilyonectria* spp. at a given sample period. ""***" indicate overall significant (0.001, respectively) positive or negative effects of a factor on *Ilyonectria* spp. abundance.

Irrigation type also affected *Ilyonectria* spp. abundance [$F_{(2,115)} = 9.51$, $P < 0.001$], with both dual and sprinkler irrigation leading to greater abundance overall compared to drip irrigation, though the strength of this effect depended on sampling period (**Figure 4**).

DISCUSSION

Groundcover vegetation was related to the abundance of both soil fungal guilds studied. As expected, native plants were associated with greater amounts of EP fungi, suggesting that coadaptation may promote positive plant soil feedback through improved herbivore control and plant protection. The positive effect of legumes on EP fungi also matched our predictions, though there were no consistent effects of legumes on *Ilyonectria* spp. Instead, *Ilyonectria* spp. were mostly deterred by the presence of grasses and native species, further suggesting that native species could play a role in promoting positive plant-soil feedbacks

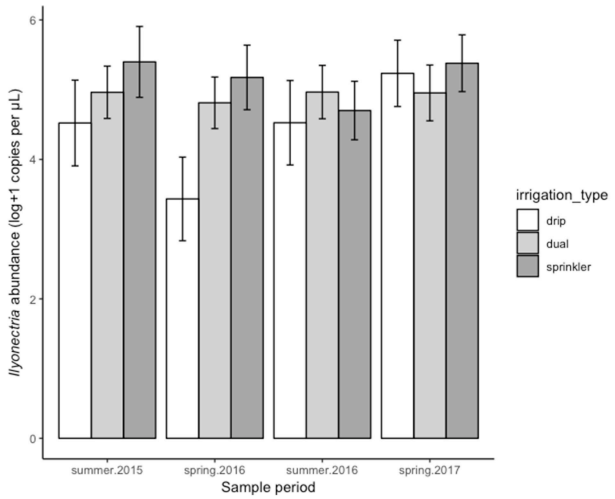

FIGURE 4 | Effect of irrigation type (shades) on *Ilyonectria* spp. abundance across all sites at four sampling periods. Error bars indicate 95% confidence limits based on likelihood of these estimates within the final model, i.e., accounting for all other factors included in the model.

in these vineyards by limiting this soil borne pathogen in this semi-arid region.

Beauveria bassiana

The increase in *B. bassiana* with locally adapted plant communities as seen in this study may have a basis in co-adaptation, as *B. bassiana* is now known to have diverged from fungi with purely endophytic lifestyles (Moonjely et al., 2016). This is, to our knowledge, the first report of a preferential association between EP fungi and native plant communities within an agricultural field. The inclusion of native species may encourage positive plant-soil feedback for crop plants such as grapevines if the larger EP fungal populations help control soil-dwelling herbivores such as climbing cutworm, mealybug, or phylloxera. To date there are no studies that specifically include EP fungi as an important player in plant-soil feedbacks, but regulation of herbivory as well as pathogen protection offered by these fungi (Ownley et al., 2010) warrant further investigation, e.g., in the context of conservation biological control (Pell et al., 2010).

The positive effect of annual species on *B. bassiana* could be because this EP fungus can persist in annually cropped fields, unlike some other EP fungi that prefer undisturbed habitats (Meyling and Eilenberg, 2006; Meyling et al., 2009; Medo and Cagan, 2011). Randhawa et al. (2018) recently showed that another common EP fungus, *Metarhizium robertsii*, occurs in higher numbers soon after disturbance and then declines with time since disturbance. Perhaps common EP fungi such as *B. bassiana* and *Metarhizium* spp. are most dominant in annual agricultural fields due to some unknown adaptation to physical disturbance, annual and weedy plant species, or the insect communities that occur in these disturbed habitats (e.g., ground-dwelling decomposers).

The increase in *B. bassiana* with legumes as seen here is consistent with a previous finding that *B. bassiana* persists well in legume cover crops in orchards (Shapiro-Ilan et al., 2012), although that study only compared legumes to the absence of a cover crop. Because legumes had a positive influence on *B. bassiana* in our large dataset looking at many different plant traits, this hints at some functional attribute of legumes that is especially beneficial for the success of *B. bassiana*. Most EP fungi including *B. bassiana* are poor competitors as saprotrophs (Meyling and Eilenberg, 2007), ruling out the effect of high litter quality of legumes. Most likely the benefits of a legume for EP fungi lie either in the attractiveness of the legume roots to soil herbivores (Schallhart et al., 2012), their suitability for endophytic colonization by EP fungi (Behie et al., 2015), protection from environmental stresses (Shapiro-Ilan et al., 2012) or some combination of these. The higher litter N quality of legumes may also attract more soil-dwelling insects (House and Alzugaray, 1989), thus indirectly increasing EP fungi.

Organic matter was positively associated with *B. bassiana* abundance at most sampling periods. A positive correlation between organic matter and the organisms that contribute to its formation can be expected (Kallenbach et al., 2016). There are several studies that show greater EP fungal isolation associated with higher organic matter soils (Ali-Shtayeh et al., 2003; Medo and Cagan, 2011) and organic fertilization (Clifton et al., 2015). Because *Beauveria* are generally poor competitors as saprotrophs, it is unlikely that there is a direct effect of organic matter on their populations. Instead, higher organic matter is likely associated with greater biological activity in general, including more plant roots and insects, both of which are hosts for these fungi.

Ilyonectria spp.

The decrease in *Ilyonectria* spp. with grass cover is consistent with the small amount of peripheral work on the effect of non-crop vegetation on these pathogens. For example, although a survey of vineyard weeds by Agustí-Brisach et al. (2011) found *Ilyonectria* spp. in many common weeds, only six species of grass were included in that study, of which only two hosted *Ilyonectria* spp. In studies of replant disease of apple, Mazzola et al. (2004) were able to reduce damage caused by pathogens such as *Ilyonectria* spp. through stimulation of an antagonistic rhizobacteria population using a wheat cover crop. Other grasses, such as *Lolium perenne*, have also been implicated in promoting bacteria with fungistatic genes (Latz et al., 2015), suggesting that perhaps some grasses deter these generalist pathogens by culturing an antagonistic rhizosphere community and thus are not good hosts. Although these potential mechanisms are speculative, the consistency of our results suggest that grasses are somehow poorer hosts for *Ilyonectria* spp. in these vineyards than broadleaves and might then promote positive plant-soil feedback by deterring generalist pathogens.

Exotic plants tended to increase *Ilyonectria* spp. abundance overall, but this was due to the strong effects seen only during spring sampling periods. It could be that this pathogen thrives in cultivated plants and associated weedy species, which are mostly exotic species in the studied region. Work on invasive plant species has shown that generalist pathogens can build up on

exotic species with negligible effects on those plants (Mangla and Callaway, 2008). If *Ilyonectria* spp. accumulates on exotic plants, this may lead to negative feedback on vines sharing the same soil through a spillover effect. A possible explanation for the springtime effects of exotic plants on *Ilyonectria* spp. abundance could be that many of the exotic weedy species may be more active in the spring.

As with *B. bassiana*, *Ilyonectria* spp. was positively related to soil organic matter, perhaps relating to the general microbial contribution to stable organic matter (Kallenbach et al., 2016). This increase in *Ilyonectria* spp. with greater amounts of organic matter is not necessarily an indication of increased disease pressure for crop plants occupying this soil because increased microbial competition and antagonism also occurs with the use of organic amendments(Bonanomi et al., 2007; Watson et al., 2017).

The increase in *Ilyonectria* spp. with supplemental irrigation could be expected given that *Ilyonectria* spp.-related diseases such as black foot disease of grape tend to be more problematic with prolonged periods of excessive soil moisture (Halleen et al., 2006). It is also likely that the use of sprinkler irrigation leads to broader distribution of grapevine roots throughout the vineyard floor. As grapevines are good hosts for these fungi, the proximity of vine roots to the drive row sample plots could have also contributed to this effect in addition to the increased frequency of wetting.

CONCLUSION

This study is the first to investigate the relationships between groundcover plant community characteristics as well as soil and irrigation factors on the abundance of the entomopathogenic *B. bassiana,* and the plant pathogenic *Ilyonectria* spp.. We conclude that native species may play an important role in managing plant-soil feedbacks in perennial agroecosystems as they promoted the plant-beneficial fungi *B. bassiana* but deterred the plant-pathogenic *Ilyonectria* spp. Practical application of this work will require further studies linking these plant-induced changes to soil fungi with measurable plant-soil feedbacks along with continued field trials to find locally adapted species best suited for use in perennial agricultural groundcovers.

AUTHOR CONTRIBUTIONS

EV performed all data collection, laboratory analysis, and manuscript preparation. DL maintained experimental field plots, identified potential sample sites, and gave feedback on the manuscript. JB performed statistical analysis. MH provided laboratory resources, extra student help, and feedback on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00118/full#supplementary-material

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