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Cultivation and domestication of highbush blueberry (*Vaccinium corymbosum*) alters abundance, diversity and virulence of entomopathogenic nematodes

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ABSTRACT

We investigated the interactive effect of plant domestication and perennial cultivation on abundance, diversity and virulence of entomopathogenic nematodes (EPN) associated with highbush blueberry (*Vaccinium corymbosum*). The rhizospheric soil of *V. corymbosum* plants was sampled in coupled wild and cultivated sites within the Pinelands National Reserve, New Jersey, USA from 2011 to 2013 at three points during each year. To isolate and assess abundance of EPN communities, soil samples were baited with wax moth larvae (*Galleria mellonella*). A subsample of EPNs isolated from the soil was identified using molecular barcoding. The virulence of three native isolates against oriental beetle, *Anomala orientalis*, larvae was assessed at multiple densities of nematodes per host. A cursory assessment of EPN diversity was based on variation in molecular barcodes because many sequences could not be identified in the genomic database GenBank. The variation among barcodes suggested that diversity was higher in rhizospheric soil associated with wild plants than that of cultivated fields. *Steinernema glaseri* was the only EPN species able to be identified using molecular methods and was the only species isolated from the six cultivated fields with EPN presence. An interaction of environment, sampling point, and year explained significant differences in EPN abundance in 2011 and 2012 when soil samples were assessed by plant. However, in 2013, soil was assessed by field rather than plant and our results show EPN abundance was higher in cultivated than in wild sites. Soil nutrients and characteristics were also assessed in 2013. A PCA analysis of soil characteristics linked higher plant nutrients to soil from cultivated fields and higher soil moisture, organic matter, boron and lower pH to wild plant-associated soil. In this study, cultivation of domesticated *V. corymbosum* increases the abundance of the more virulent EPN species against the presumed host, *A. orientalis* but appears to eliminate genetic variability from the EPN community.

1. Introduction

The development of sustainable approaches to soil conservation necessitates an increased understanding of how land management practices impact the services soil can provide for humans and others (Doran, 2002). Agricultural production of plants is known to change the abundance and diversity of communities of aboveground insect herbivores and their predators and parasitoids (Matson et al., 1997; Poelman et al., 2008). It is difficult, however, to determine the true effect of plant domestication and land alteration for agricultural use on interactions in the agroecosystem without investigation of and comparison to undisturbed wild populations of plants; this is especially true for associated soil communities held in delicate balance with one another.

Nematodes are diverse and prevalent throughout soil communities worldwide. Within this taxon many feeding habits are found that occur at multiple trophic levels making nematodes an excellent bioindicator of disturbance to the soil ecosystem (Bongers and Ferris, 1999; Bongers, 1990; Yeates et al., 1993). Thus, the diversity of nematode species present is often used to evaluate the effects of land management practices

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(Freckman and Ettema, 1993; Millar and Barbercheck, 2002; Morise et al., 2012). The effect of altered soil structure through agriculturally focused land management on nematode communities is well studied and the effects of disturbance for this purpose (e.g., tillage, perennial or annual cultivation) are relatively clear (Erb and Lu, 2013; Govaerts et al., 2007; Sánchez-Moreno and Ferris, 2007; Vonk et al., 2013). In spite of this, the disturbance of soil is only a single factor in the alteration of land for agricultural production.

Alongside soil disturbance, plant domestication and the subsequent establishment of large plant monocultures are two other notable modifications to the land caused by agricultural production. Increasingly, plant genotype and species identity is being linked to the diversity and functionality of soil communities (Bezemer et al., 2010; Kostenko et al., 2015; Van der Putten et al., 2001; Wardle et al., 2003; Zak et al., 2003). Plant domestication is largely based on the artificial selection and enhancement of human-desired traits. The consequent changes to a plant's genome are substantial due to selection from a relatively small population of plants (i.e., genetic drift) which causes continued bottlenecking as a limited diversity of plant stock is used for breeding to accentuate specific traits (Chen et al., 2015). This can cause indirect and sometimes negative effects on the plant's ability to respond and defend itself against belowground attacks (Chen et al., 2015; Degenhardt et al., 2009). As knowledge of the connection between above and belowground interactions expands, the effect of cultivation and plant domestication on soil organisms has become a point of interest (Palomares-Rius et al., 2015; Rivera et al., 2015; Sánchez-Moreno and Ferris, 2007). While the impact of plant domestication has been assessed previously, usually indirectly, it is often hard to access wild populations of plants at their point of origin to directly study the effects of domestication and cultivation. This study investigates the effect of domestication and cultivation on nematodes that feed at the third trophic level, i.e., entomopathogenic nematodes (EPN) with the hypothesis that the dynamics of the belowground arena would mirror effects found in the aboveground arena with higher trophic levels being more responsive to disturbance (Jonsson et al., 2012).

EPNs are obligate parasites of soil-dwelling insects and other arthropods. In natural systems, EPNs can have significant top–down effects on insect populations (Strong et al., 1996) and thus, in agricultural systems, are considered promising biological control agents for insect pest control (Denno et al., 2008; Gaugler et al., 1997). EPNs are active in the soil only as infective juveniles (IJs) that carry with them a symbiotic bacterium released inside an insect host to cause septicemia. The IJ is a special dauer-like stage that is non-feeding but persists in the soil until a host is located. Upon locating a host, the IJ must then enter the host through any opening (e.g., mouth, anus, spiracles etc.). Once inside the host's body cavity, the bacterium is released and the success of the EPN is dependent on the ability of the bacterium-nematode complex to overcome the insect's immune system. A successful infection will result in up to three EPN life cycles occurring in the cadaver as they feed on the multiplying symbiotic bacteria and host tissues broken down by the bacteria. Once resources in the cadaver are depleted, hundreds to hundreds of thousands of IJs exit into the surrounding soil and search for a new host. This search is directed by a variety of cues such as carbon dioxide and other volatile organic compounds emitted by insects (Lewis et al., 1993, 2009) and by plant roots (Turlings et al., 2012). Because EPN respond to cues from soil insects and plant roots, we hypothesized that diversity and functionality of EPN communities would diverge between wild and cultivated plants of the same species.

We used the highbush blueberry (*Vaccinium corymbosum* L.) agroecosystem in southern New Jersey, USA to explore the effects of plant domestication on belowground interactions. This system is quite unique in that *V. corymbosum* was first domesticated and grown commercially there in the early twentieth century. As a result of its recent domestication, wild and cultivated multispecies hybrids of *V. corymbosum* are still considered the same species (Bian et al., 2014; Eck, 1965). In contrast, many domesticated plants are such severe mutants of their parental lines they can no longer function as the same species (i.e., cannot successfully cross-pollinate one another to produce viable offspring). Relatively shortly after commercial production began, legislation was put into effect that protected the wild plants in the unique ecosystem surrounding this region. The legislation was established in 1978 as the United States National Parks and Recreation Act, which denoted the area as the "Pinelands National Reserve" (boundaries shown in Fig. 1). This spurred the later and local 1979 New Jersey Pinelands Protection Act, that regulates the boundaries, land management and minimum standards for land use within the Pinelands National Reserve (Pinelands Facts, 2016; Pinelands Comprehensive Management Plan, 2014). This legislation acknowledges the economic importance and cultural connection of blueberry and cranberry production in this region by classifying areas within the reserve as "Special Agriculture Production Areas". These two acts mandated the preservation of wild stands in this region and uniquely allowed for the production of domesticated cultivars nearby protected wild stands, making this an ideal system to study the interactive effects of cultivation practices and plant domestication on EPN communities. The objective of this study was to compare EPN diversity and functionality of EPN

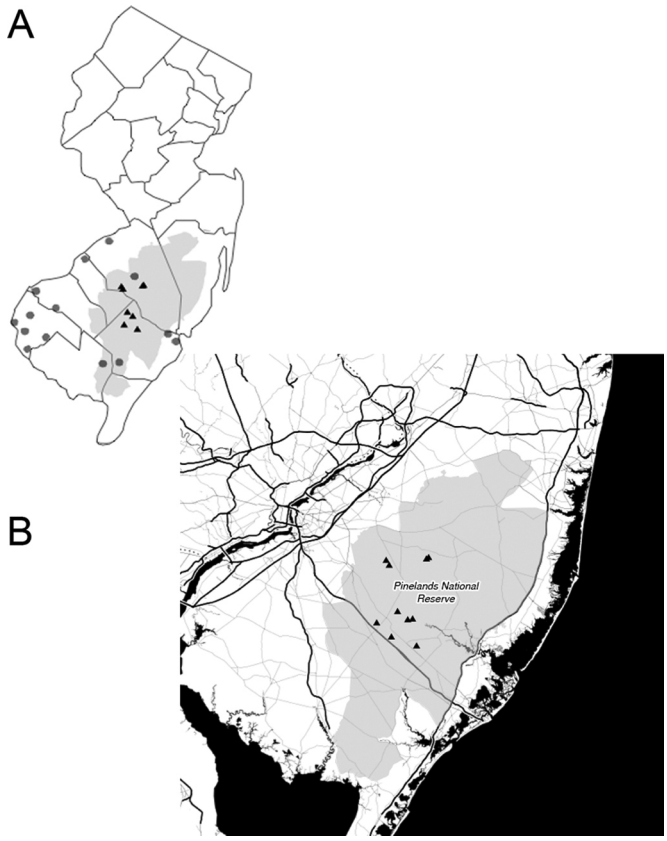

Fig. 1. Distribution of entomopathogenic nematode sampling sites in wild and domesticated stands of *Vaccinium corymbosum* within the Pineland National Reserve (PNR) in New Jersey, USA. Panel A shows sites positive for *Steinernema glaseri* (solid black circles) in an extensive sample of the state of New Jersey (Gaugler et al., 1992), and sites used in this study with positive infections (solid black triangles). Panel B shows a more detailed map of the location within the PNR.