



Effects of environmental and agronomic factors on soil-dwelling pest communities in cereal crops



Ivan Milosavljević^{a,*}, Aaron D. Esser^b, David W. Crowder^a

^a Washington State University Entomology, 166 FSHN Bldg, Pullman, WA 99164, United States

^b Washington State University Extension, 210 W Broadway, Ritzville, WA 99169, United States

ARTICLE INFO

Article history:

Received 6 November 2015
Received in revised form 14 March 2016
Accepted 14 April 2016
Available online 29 April 2016

Keywords:

Elateridae
Wireworms
Species distribution
Climatic factors
Integrated pest management

ABSTRACT

Characterizing the composition of pest communities across variable cropping landscapes is critical for developing integrated management programs due to variation across species in their ecology and impacts on crops. Wireworms, the soil-dwelling larvae of click beetles, have resurged as major pests of cereal crops in the Pacific Northwestern United States, but knowledge of the composition of wireworm communities across cereal-growing landscapes remains limited. Here, we conducted a large-scale field survey of wireworms across a broad region in the Pacific Northwest. We identified a total of 13 wireworm species across samples taken from 160 fields in Washington, Oregon, and Idaho. The most common species were *Limonius infuscatus*, *L. californicus*, and *Selatosomus pruininus*, which together represented approximately 90% of collected larvae. Wireworm communities were more abundant and diverse in spring wheat and conservation reserve program compared with winter wheat fields. Interestingly, *L. californicus* was the only species that was more abundant in cultivated wheat crops than in native grass fields, suggesting that this species persists in crop habitats throughout its life cycle and thus might exert stronger impacts on winter crops compared to other species. Our results indicate that *Limonius* species are distributed mostly in the intermediate and higher precipitation zones or in irrigated fields, while *S. pruininus* is confined to drier regions. As the dominant wireworm species, the diversity of wireworm communities, and total wireworm abundance varied across crops, landscapes, and climatic regions, management practices should vary across regions for maximum effectiveness.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

The distribution and abundance of pest species in agroecosystems are governed by many environmental and agronomic factors (Pedigo and Rice, 2008; Ehrlén and Morris, 2015). Understanding which factors mediate the persistence of pest species and their population dynamics is in turn an essential principle of sustainable pest management (Pedigo and Rice, 2008; Price et al., 2012). Agricultural landscapes often vary considerably in terms of habitat composition and other environmental conditions, and characterizing which environmental factors and management practices promote abundant and diverse pest communities is critical for the development of effective control tactics (Pedigo and Rice, 2008; Price et al., 2012).

Wireworms, the soil-dwelling larvae of click beetles (Coleoptera: Elateridae), have re-emerged as economically significant

pests of cereal, vegetable, and legume crops in the Pacific Northwestern United States (PNW) (Higginbotham et al., 2014; Esser et al., 2015; Milosavljević et al., 2016). Wireworms were considered severe crop pests in the early 20th century (Comstock and Slingerland, 1891), but dwindled in importance beginning in the 1950's due to the effectiveness of potent broad-spectrum insecticides used for their control (Vernon et al., 2008). Reliance on these chemicals created a false sense of security and decreased growers' awareness of wireworms (van Herk and Vernon, 2007; Vernon et al., 2009), resulting in scant research on the biology and ecology of wireworms for nearly 40 years (Traugott et al., 2015). When several broad-spectrum pesticides were removed from the market and replaced by less effective second-generation toxins, however, wireworms resurged as problematic pests of many field crops (Parker and Howard, 2001; Hermann et al., 2013). Unfortunately, producers are faced with this challenge without the basic knowledge to develop efficient management plans. This has threatened the productivity of agricultural systems in the PNW and globally.

* Corresponding author.

E-mail address: ivan.milosavljevic@wsu.edu (I. Milosavljević).

Substantial temporal and spatial variability in the composition of wireworm communities has made sampling and identification difficult, hampering the development of management strategies (Blackshaw and Vernon, 2006; Willis et al., 2010). Recognizing which wireworm species of economic significance are likely to occur in a given region, or which factors might promote outbreaks in a given field, are thus extremely important (Traugott et al., 2008, 2015; Benefer et al., 2012; Barsics et al., 2013). Within fields, food availability, crop rotations, and agronomic conditions mediate the abundance of wireworms (Furlan, 2004; Jung et al., 2014). Soil characteristics are also important, with studies showing that factors such as texture, moisture, pH, temperature, bulk density, and organic matter impact wireworms (Thomas, 1940; Lefko et al., 1998; Kovács et al., 2006; Hermann et al., 2013; Staudacher et al., 2013).

At broader landscape scales, the availability of habitats that are suitable for oviposition, reproduction, and overwintering, such as grasslands, can impact wireworm abundance (Lefko et al., 1998; Furlan, 2004; Kovács et al., 2006; Keiser et al., 2012; Hermann et al., 2013). The proximity of grasslands to crop fields can also affect dispersal into crops and overall wireworm abundance, although impacts have been shown to be species-dependent (Toepfer et al., 2007). In Europe, predictive models have been developed that relate factors such as cropping landscapes and soil characteristics (i.e. moisture, temperature, type) to wireworm abundance. These models have been shown to predict up to 89% of the variability in wireworm abundance in given fields (Hermann et al., 2013; Jung et al., 2014). As the distribution of wireworm species varies across the PNW (Lane, 1925; Glen, 1950; Toba and Turner, 1983; Toba and Campbell, 1992), such models would help identify areas where damaging wireworm species are likely to occur. Previous research has shown that different wireworm species have variable responses to control treatments, such that economic thresholds vary across species (Furlan, 2004, 2014; Esser et al., 2015). In turn, models that predict wireworm abundance, when combined with knowledge of particular species occurring in a given region, could substantially improve wireworm IPM.

Here, we conducted a large-scale survey to characterize the distribution and community composition of wireworm species infesting cereal crops and native grasslands in the PNW. Wireworms continue to pose a serious threat to wheat (*Triticum aestivum*) production in the PNW, with up to 70% yield losses (Reddy et al., 2014). First, we examined whether the abundance, diversity, and composition of wireworm communities differed in wheat cropping systems compared with conservation reserve program (CRP) fields that contain native grasses. We also evaluated how wireworm community structure was affected by environmental and agronomic factors across our broad study region. Our goal was to determine the primary factors mediating wireworm abundance and community structure. This could provide a more solid foundation for IPM, because if growers can accurately assess which species will likely be present in their fields, they could incorporate this information into their risk assessment (Furlan, 2014).

2. Materials and methods

2.1. Study sites

In 2013 and 2014, we developed an extensive sampling network to document the distribution of wireworms in commercial wheat fields and native grasslands in the PNW. This network consisted of 160 fields distributed across 20 counties in Washington, Oregon, and Idaho (Fig. 1). Each year we sampled 40 spring wheat (SW) fields, 20 winter wheat (WW) fields, and 20 Conservation Reserve Program (CRP) fields. All CRP fields contained native grasses and

had not been planted to crops for over 10 years. We sampled CRP sites in addition to wheat fields because native grasses might serve as sources of wireworms and adult beetles that could migrate into adjacent crop fields. All of the fields were located in 150–750 mm annual precipitation zones (AgWeatherNet, 2015) with soil types ranging from sandy loam to silty clay loams.

All crop fields were managed by participating growers, following practices typical of the PNW region (Camara et al., 2003). Representative wheat growing practices of the region include intensive large-acreage monoculture cropping systems (Schillinger and Papendick, 2008). In areas with lower precipitation, standard rotational practices comprise of two-year rotations of winter wheat-spring wheat or winter wheat-summer fallow. Common rotations in higher rainfall zones include three-year rotations of winter wheat-spring wheat-spring wheat/barley, winter winter-spring wheat-summer fallow, or winter wheat-spring wheat-legume (Schillinger et al., 2006). Fifty of the wheat farms in our study used no-till production methods while the other 70 used conventional tillage practices (Schillinger and Papendick, 2008). Each surveyed farm used seed-applied neonicotinoid insecticides (i.e. thiamethoxam and imidacloprid) at rates between 7 and 12 g active ingredient per 100 kg seed for the control of early-season pests in cereal crops.

2.2. Insect sampling and identification

Wireworm larvae were sampled using modified solar bait traps (Esser et al., 2015). In each field, 10 baits were deployed once in the spring when soil temperatures reached 6 °C. This corresponds with the temperature at which we have observed wireworms start actively feeding on cereal crops in our region (Milosavljević, personal observation). Each bait trap consisted of a nylon stocking filled with 120 cm³ of wheat and corn seeds in a 50:50 ratio. Traps were kept submerged in water for 24 h prior to deployment to encourage seed germination; germinating seeds produce and emit elevated amounts of CO₂ that are attractive to wireworms (Doane et al., 1975; Doane and Klingler, 1978; Johnson and Nielsen, 2012). A study area measuring 400 m × 250 m (10 ha) was established in each surveyed field (Fig. 2). The first bait was set up 50 m from a field edge to limit edge effects, and subsequent baits were placed in a zig-zag pattern moving into the field, with approximately 50 m between traps (Fig. 2). Each trap was deployed in 20 cm deep hole in the ground, covered with sufficient soil, and flagged to allow easy retrieval. In addition to flags, we covered each trap with a clear and black plastic cover (90 × 90 cm in size) which helped warm the ground and speed up germination. All traps were retrieved after 8 days and transported to the laboratory where they were assessed for wireworms by hand.

Collected larvae were identified to species based on morphological characteristics (Glen et al., 1943; Lanchester, 1946). To ensure that our identifications were accurate, we identified a subset of individuals of each species using DNA barcoding methods (Etzler et al., 2014). This was performed on 5 individuals of the three most prevalent species and 2 individuals of each of the other species from each of several different geographic locations. Each specimen was cut between the second and third abdominal segment to extract DNA. Then, the mitochondrial cytochrome oxidase I (COI) gene was sequenced and compared to existing species (Folmer et al., 1994; Lindroth and Clark, 2009; Staudacher et al., 2011; Etzler et al., 2014).

2.3. Collection of environmental and management data

We recorded data on environmental and agronomic factors at each farm to determine their effects on wireworm communities. These factors were: (1) accumulated rainfall within 30 days of

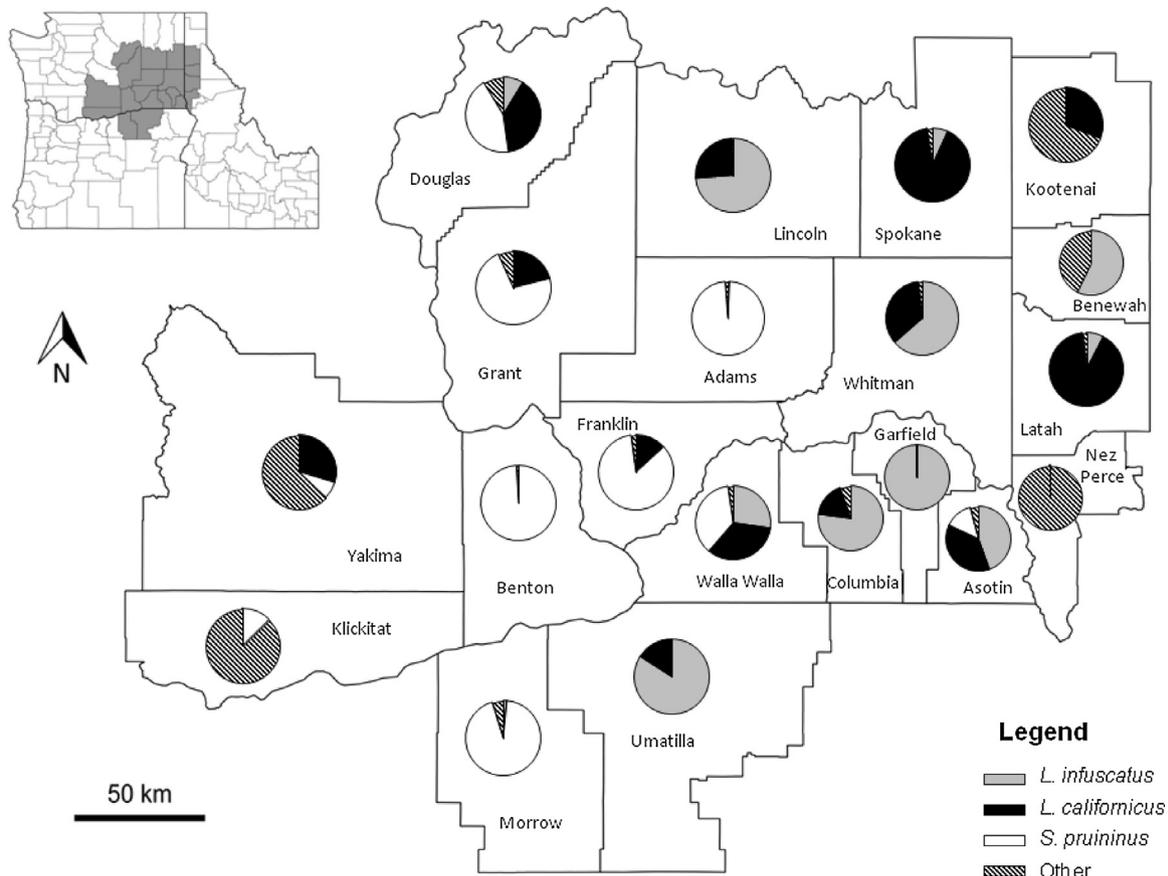


Fig. 1. Map showing the composition of wireworm communities across counties. Circles indicate proportions of species collected in each county. Light gray color denotes *L. infuscatius*, black color denotes *L. californicus*, white color describes *S. pruininus*, and pattern texture denotes other species collected in 2013 and 2014.

wireworm sampling, (2) soil temperature, (3) soil pH, (4) soil moisture, (5) soil texture (% silt, clay, sand), (6) field type (spring wheat, winter wheat, CRP), (7) previous crop (grass or non-grass), and (8) tillage (conventional or no-till). Rainfall data for each field were obtained from the closest weather station (AgWeatherNet, 2015). Soil sensors were used on-site to measure soil factors such

as temperature (Luster Leaf® Rapitest Digital Soil Thermometer), pH (Luster Leaf® Rapitest Digital Soil pH Meter), and moisture content (General® Digital Soil Moisture Meter with a probe, 20 cm long). To determine soil texture, approximately 240 cm³ of soil was taken from the bottom of each hole where wireworms were sampled. These samples were placed in plastic bag and mixed to homogenize them. Bags were put on ice in portable coolers, and transported to the laboratory. Prior to the assessment, samples were kept stored in the walk-in refrigerator at -4 °C. Samples were analyzed using standardized analytical methods for relative proportions of clay, silt, and sand (Smith and Mullins, 1991; Taubner et al., 2009). The previous crop in each field and tillage practices were obtained directly from participating growers.

2.4. Data analyses

To analyze whether wireworm abundance and diversity were affected by environmental and agronomic factors we used linear mixed-effects models, followed by model selection. Fixed effects in the initial models included percentage of sand, percentage of silt, crop type, tillage, soil temperature, soil moisture, soil pH, previous crop, and cumulative rainfall within 30 days of sampling. Random effects included year and site identity. Separate models were conducted for each of the five response variables (total wireworm abundance, number of wireworm species, abundance of *L. infuscatius*, abundance of *L. californicus*, and abundance of *S. pruininus*). All models for abundance were fit with a negative binomial distribution based on the distribution of the count data;

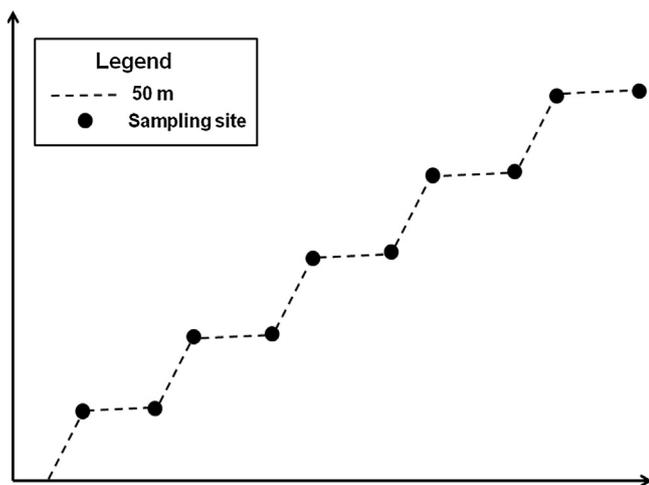


Fig. 2. Insect sampling plan per field. Dashed lines indicate distance of 50 m between two sampling sites. Black circles denote sampling locations in each field surveyed in 2013 and 2014.

the model for wireworm species richness was fit with a normal distribution.

For each response, we used stepwise regression to reduce the number of fixed effects in the models (Crowder et al., 2010), because multi-collinearity among the explanatory variables (for example rainfall and soil moisture) would have violated model assumptions if all explanatory variables were used (Kutner et al., 2005). We used backwards stepwise regression, where model selection started with all nine variables, and in each backward step we removed the variable with the lowest χ^2 statistic (Kutner et al., 2005). We used a conservative criterion ($\alpha = 0.15$) to ensure that any variables not retained would not significantly affect parameter estimation. After models were selected, we performed lack-of-fit tests (Kutner et al., 2005) to determine whether the model with fewer variables fit the data worse than the full model. We also performed model selection with information criteria (Akaike's information criterion) (Whittingham et al., 2006; Crowder et al., 2010), and found results matched those from stepwise regression. These analyses were performed in SAS (SAS Institute, 2012).

3. Results

3.1. Distribution of wireworm species

87% of the 160 fields surveyed for wireworms had at least one individual collected. From these fields, a total of 3311 wireworm individuals were collected and 13 species were identified (Table 1). We found no discrepancies in our visual and DNA-based identification methods. Wireworm communities across the PNW region were dominated by only three species, *Limonium infuscatus*, *L. californicus*, and *Selatosomus pruininus*, which together represented 41%, 28%, and 21% of collected individuals, respectively. The dominant species varied across counties, suggesting that landscapes, environmental factors, and agronomic variability affected wireworm community structure (Fig. 1).

3.2. Effects of environmental and agronomic factors on overall wireworm community

Total wireworm abundance was impacted by crop, soil texture, and soil temperature; other variables did not significantly affect model fit (lack of fit test, $F_{6,149} = 0.44$, $P = 0.85$). More wireworms were collected in spring wheat and CRP fields than in winter wheat crops (Table 2A, Fig. 3A). Moreover, the total abundance of wireworms increased significantly with higher soil temperatures (Table 2A) but decreased with more sandy soils (Table 2A). The species richness of wireworms was impacted by crop type, soil texture, and soil pH; other variables did not affect model fit and

Table 1

Wireworm species collected in Washington, Oregon, and Idaho in 2013 and 2014. Shown are the species, number of larvae, and percentage of total larvae collected.

Species	Number of collected larvae	%
<i>Limonium infuscatus</i> Motschulsky	1359	41.0
<i>Limonium californicus</i> (Mannerheim)	917	27.7
<i>Selatosomus pruininus</i> (Horn)	689	20.8
<i>Hadromorphus glaucus</i> (Germar)	196	5.9
<i>Dalopius asellus</i> Brown	75	2.27
<i>Aeolus mellillus</i> (Say)	32	0.97
<i>Hypnoidus bicolor</i> (Eschscholtz)	18	0.54
<i>Sylvanelater limoniiiformis</i> Horn.	11	0.33
<i>Selatosomus aeripennis</i> (Kirby)	4	0.12
<i>Ampepus</i> sp.	3	0.091
<i>Melanotus oregonensis</i> (LeConte)	3	0.091
<i>Agriotes</i> sp.	2	0.060
<i>Hemicrepidius</i> sp.	2	0.060

Table 2

Results of linear mixed-effects models testing the effects of multiple environmental and management variables on (A) the total abundance of wireworms and (B) the number of wireworm species present. Stepwise regression and lack-of-fit tests were used to select a subset of variables retained in the final model, and only these variables are shown. **: $P < 0.05$; ***: $P < 0.01$.

A				
Abundance	Estimate	SE	χ^2	P
Crop	N/A	N/A	23.65	<0.0001***
Percentage of sand	-0.025	0.0076	9.80	0.0017***
Soil Temperature	0.29	0.086	11.14	0.0008***
B				
Species richness	Estimate	SE	F	P
Crop	N/A	N/A	12.82	<0.0001***
Percentage of silt	0.0034	0.0022	2.46	0.12
Soil pH	0.21	0.10	5.72	0.018**

were removed from our model (lack of fit test, $F_{6,149} = 0.19$, $P = 0.98$). Wireworm diversity was lowest in winter wheat crops (Fig. 3B). Wireworm species diversity also increased significantly with higher soil pH ($F_{1,150} = 2.36$, $P = 0.018$; Table 2B).

3.3. Effects of environmental and agronomic factors on common wireworm species

The abundance of *L. infuscatus* was impacted by crop type and soil texture; other variables did not significantly affect model fit (lack of fit test, $F_{7,149} = 0.53$, $P = 0.81$). This species was negatively affected by the percentage of sand ($\chi^2 = 17.43$, $P < 0.0001$) in soils (Table 3A). Winter wheat fields had fewer *L. infuscatus* than spring wheat and CRP fields, although this effect was only marginally significant ($\chi^2 = 5.65$, $P = 0.059$) (Fig. 4A). The abundance of *L. californicus* was impacted by crop type, soil moisture, and soil pH; other variables did not significantly affect model fit (lack of fit test, $F_{6,149} = 0.082$, $P = 0.99$). This species was more abundant in spring wheat than in CRP fields ($\chi^2 = 6.50$, $P = 0.011$), but had similar abundance in spring and winter wheat ($\chi^2 = 3.24$, $P = 0.072$) (Fig. 4B). This species increased in abundance with higher soil moisture ($\chi^2 = 9.03$, $P = 0.0058$; Table 3B) and soil pH ($\chi^2 = 5.17$, $P = 0.023$; Table 3B). The abundance of *S. pruininus* was impacted by crop type, soil texture, soil temperature, and soil moisture; other variables did not significantly affect model fit (lack of fit test, $F_{5,149} = 1.57$, $P = 0.17$). This species decreased in abundance as soil moisture levels ($\chi^2 = 51.00$, $P < 0.0001$) and temperatures increased ($\chi^2 = 5.02$, $P = 0.025$) (Table 3C). Like *L. infuscatus*, *S. pruininus* was found in lower abundance in winter wheat fields compared to spring wheat ($\chi^2 = 3.94$, $P = 0.047$) and CRP ($\chi^2 = 5.40$, $P = 0.020$) (Fig. 4C).

4. Discussion

Environmental variability affects interactions between insects, plants, and the ecosystems in which they live (Price et al., 2012). Understanding how pests respond to environmental and agronomic factors is critical for developing sustainable IPM programs. To date, approximately 1000 different wireworm species have been recorded in North America (Marske and Ivie, 2003; Majka and Johnson, 2008). Yet, in general, scant information is available on the factors that mediate wireworm community structure. Our study provides novel insight on the distribution of economically important wireworm species in the Pacific Northwestern USA.

The abundance of particular wireworm species has been shown to vary considerably based on geographic location and habitat composition (Traugott et al., 2008; Staudacher et al., 2013).

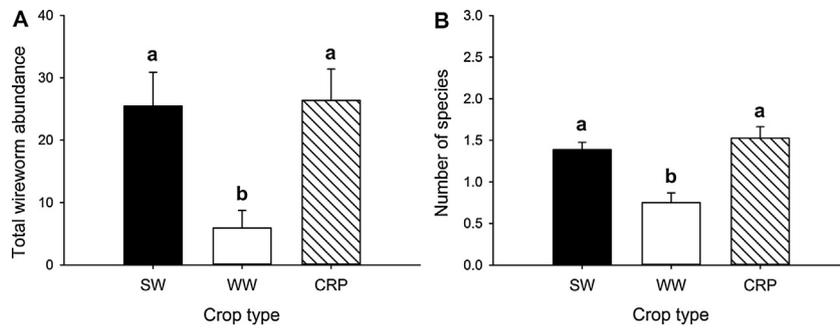


Fig. 3. The (A) total abundance of wireworms (mean number of individuals collected per ten traps + SE) and (B) the number of wireworm species collected (mean number of species collected per ten traps + SE) in three different crop types (averaged across 2013 and 2014). Shown are the values for total abundance and species richness for wireworm communities collected in spring wheat (SW), winter wheat (WW), and CRP (CRP) fields. In each panel, different letters above the bars indicate significant differences ($\alpha = 0.05$).

However, few studies have focused on identifying wireworm species in PNW farmlands, with information published to date providing inconsistent results (Lane, 1925; Glen, 1950; Toba and Turner, 1983; Toba and Campbell, 1992). One common theme that emerged from earlier studies was that wireworm communities in the PNW are dominated by few species (Lane, 1925; Gibson, 1939; Shirck, 1945; Toba and Turner, 1983; Horton and Landolt, 2002). Similarly, our study revealed that wireworm communities in PNW wheat and CRP habitats were dominated by only three species. However, the overall wireworm community was quite diverse, with at least 13 total species documented. Moreover, the richness of wireworm communities varied considerably based on crop type and environmental conditions. As different wireworm species require unique management strategies (Esser et al., 2015; Milosavljević et al., 2016), our study can aid in proactively assessing which species are likely to occur in a given region. This can serve as a foundational component of developing more targeted and regionally-specific IPM approaches.

We recorded significantly fewer wireworms in winter wheat compared to spring wheat or CRP fields. As wireworms in the genera *Limoni* and *Selatosomus* spend multiple years in the soil (Lane, 1925; Lanchester, 1946), and are fairly immobile, their distributions are likely to be mediated by factors affecting adults (Parker and Seoney, 1997). Prior research has shown considerable variation in oviposition preferences of adult Elaterid beetles, which

can affect wireworm distributions (Thomas, 1940; Traugott et al., 2008; Willis et al., 2010). In the PNW, spring wheat often follows winter wheat in crop rotations, whereas winter wheat commonly follows legumes or summer fallow. The relatively high abundance of wireworms observed in spring wheat and CRP may therefore be a product of egg-laying preferences for wheat and grasses, whereas the relatively low abundance in winter wheat may reflect avoidance of egg-laying in legumes or fallowed fields. Crop rotation options are fairly limited in our study region (Schillinger et al., 2006), but our results suggest that rotations that include non-wheat crops or fallow (Esser et al., 2015) may help to lower wireworm abundance in subsequent wheat crops.

Feeding activity might also help explain differences in wireworm abundance across plant types, rather than innate wireworm preferences for oviposition sites. Winter wheat crops are well established when soil temperatures reach 6–10°C in the spring, whereas spring wheat crops are being planted. Well established winter wheat stands could attract wireworms and make bait trapping less effective (Milosavljević et al., 2016), which could in part explain lower differences in winter wheat compared to spring wheat. Variation in feeding activity could also impact the potential damage caused by wireworms. We have found that *L. californicus* larvae feed more aggressively as the crop season progresses (Milosavljević et al., 2016). Thus, damage caused by this species can amplify over the course of the season, such that early-season sampling alone is unlikely to be effective for guiding insecticide-treatment decisions. In contrast, feeding activity of *L. infuscat* declines rapidly from April to June as temperatures increase (Milosavljević et al., 2016). Thus, early-season sampling of this species is more likely to reflect the peak period of feeding activity, providing a more effective guide for treatment decisions. A better understanding of seasonal variation in feeding ecology among species could thus improve IPM by allowing producers to determine how effective a single early-season sample is at predicting the potential for economic damage over the course of a growing season.

Damage caused by wireworms has also been shown to increase with the acreage of grassy landscape elements (Parker and Seoney, 1997; Hermann et al., 2013). Our results similarly show that CRP fields, which are rich in native grasses, support high abundances of wireworms. Since CRP fields are generally located in close proximity to crop fields, and represent considerable acreage across the PNW, it is likely that they serve as sources of wireworms in crop fields. Moreover, the high abundance of wireworms in CRP fields suggests these habitats may be preferred egg-laying sites. Thus, adult beetles emerging from crops may disperse to CRP for oviposition. Moreover, if CRP fields are systemically infected with wireworms, it may present problems for farmers if the land is

Table 3

Results of linear mixed-effects models testing the effects of multiple environmental and management variables on the abundance of (A) *L. infuscat*, (B) *L. californicus*, and (C) *S. pruininus*. Information criteria (AIC) were used to select a subset of variables retained in the final model, and only these variables are shown. *: $P < 0.1$; **: $P < 0.05$; ***: $P < 0.01$.

A				
<i>L. infuscat</i>	Estimate	SE	χ^2	P
Crop	N/A	N/A	5.65	0.059*
Percentage of sand	-0.096	0.019	17.43	<0.0001***
B				
<i>L. californicus</i>	Estimate	SE	χ^2	P
Crop	N/A	N/A	8.44	0.015**
Soil moisture	0.25	0.082	9.03	0.0027***
Soil pH	1.04	0.42	5.17	0.023**
C				
<i>S. pruininus</i>	Estimate	SE	χ^2	P
Crop	N/A	N/A	11.75	0.0028**
Percentage of silt	-0.013	0.0077	2.79	0.095*
Soil temperature	-0.39	0.18	5.02	0.025**
Soil moisture	-0.41	0.053	51.00	<0.0001***

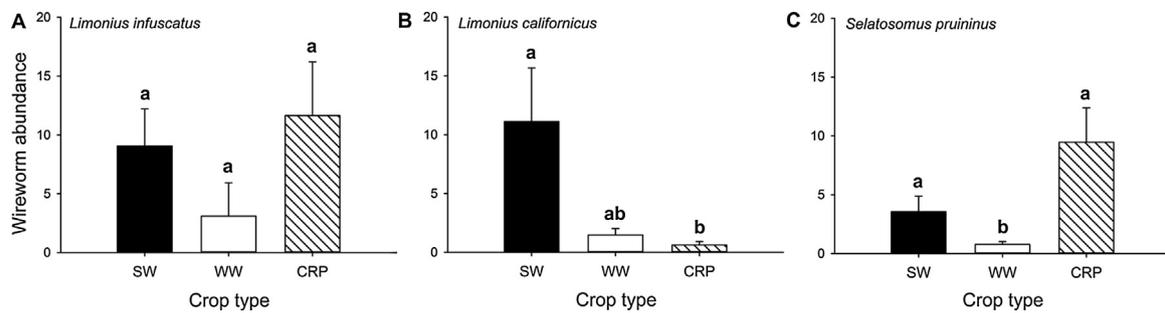


Fig. 4. The abundance of (A) *L. infuscatus*, (B) *L. californicus*, and (C) *S. pruininus* larvae collected in three different crop types (averaged across 2013 and 2014). Shown are the mean (\pm SE) for abundance of wireworms collected in spring wheat (SW), winter wheat (WW), and CRP (CRP) fields. In each panel, different letters above the bars indicate significant differences ($\alpha=0.05$).

converted back to crop production (Lefko et al., 1998). In turn, characterizing patterns of adult Elaterid dispersal between native grasslands and crops, and vice versa, may aid in our understanding of wireworm population cycles (Traugott et al., 2015).

Soil characteristics have also been shown to mediate wireworm abundance (Gui, 1935; Jones and Shirck, 1942; Villani and Wright, 1990; Furlan, 2004; Cherry and Stansly, 2008; Staudacher et al., 2013). We found that the spatial distribution of wireworms across our vast study region was mediated by soil characteristics such as texture, moisture, and temperature. For example, *S. pruininus* was mostly limited to growing areas near locations near the Cascade Mountains where annual precipitation does not exceed 300 mm and soil moisture is low. In contrast, *L. californicus* and *L. infuscatus* were primarily located in intermediate and higher precipitation zones. Farms in the PNW often have steep topography, which can affect water storage, with hill bottoms have higher moistures than hilltops (Schaeztl and Anderson, 2005; Ibrahim and Huggins, 2011). Moreover, across fields factors such as tillage can affect water storage, with no-till systems having better water storage than conventionally tilled farms that have greater erosion (Huggins and Reganold, 2008; Qiu et al., 2011). Our results suggest that such factors, which affect soil moisture both within and across fields, could impact wireworm outbreaks and long-term distributions.

We also found that more alkaline soils promoted the biodiversity of the overall wireworm community and *L. californicus* in particular. Like many agricultural areas, the PNW has growing problems with soil acidification due to rampant fertilizer use (Koenig et al., 2011). Indeed, many soils in production agricultural fields have pH below 5.0 (Koenig et al., 2011). Our results suggest that continued soil acidification could be harmful for wireworms. Soil pH can also vary widely depending on the depth where measurements are taken. For example, Koenig et al. (2011) showed that some soils with pH of 4.0 at the surface had a pH of 6.0 50 cm deep. This suggests that wireworms impacted by soil acidification may move lower in the soil profile, which could mediate their damage to crop seeds and roots growing near the soil surface.

Historically, wireworms have often been managed as a single herbivore, rather than as complex of different species (Horton, 2006; Benerfer et al., 2012). This has resulted in an overuse of environmentally hazardous insecticides over time; growers often assume that any wireworms they find are economically significant pests (Traugott et al., 2015) and that population levels are always above economic thresholds (Furlan and Kreutzweiser, 2015). Our results, however, showed that the dominant wireworm species, and the overall composition of wireworm communities, differed dramatically across the region. Our finding provides a first step towards understanding the environmental and agronomic factors that promote the abundance of particular wireworm species in the PNW. This could aid growers in proactively assess risk associated

with each species, based on their geographic location and particular conditions in their crop fields. Moreover, understanding relationships between specific agronomic practices and environmental conditions that promote wireworm outbreaks could form the foundation for more targeted and effective management strategies in the future.

5. Conclusions

Our study rigorously documented the composition of wireworm communities across variable landscapes in the PNW United States. Soil characteristics (e.g., texture, pH, moisture, temperature), rainfall, and plant species were the dominant factors governing the spatial distribution and abundance of wireworm species across the region. In general, we found that spring wheat and CRP fields had higher wireworm abundance than winter wheat. This likely reflects egg-laying preferences of adult Elaterid beetles, who prefer to lay eggs in wheat crops (which typically precede spring wheat in rotations) rather than legumes or summer fallow (which typically precede winter wheat). We also found native CRP grasslands supported high wireworm abundances, likely because these habitats are maintained with continuous grassy species. Overall, our results show how wireworm communities, and the abundances of particular species, can be mediated by environmental and agronomic variables.

Acknowledgements

We thank all the growers who provided access to their fields to conduct this survey. Thanks also to Frank Etzler, Kevin Wanner, and Michael Ivie for conducting barcoding verification of our specimens. We also thank John Reganold for help with soil analyses. This project was supported by grants from the Washington Grain Commission to DC and AE.

References

- AgWeatherNet, 2015. Washington State University's AgWeatherNet. Prosser, WA, USA. <http://weather.wsu.edu/awn.php>. (accessed 31.10.15.).
- Barsics, F., Haubruge, E., Verheggen, F.J., 2013. Wireworms' management: an overview of the existing methods, with particular regards to *Agriotes* spp. (Coleoptera: elateridae). *Insects* 4, 117–152.
- Benerfer, C.M., Knight, M.E., Ellis, J.S., Hicks, H., Blackshaw, R.P., 2012. Understanding the relationship between adult and larval *Agriotes* distributions: the effect of sampling method, species identification and abiotic variables. *Appl. Soil Ecol.* 53, 39–48.
- Blackshaw, R.P., Vernon, R.S., 2006. Spatiotemporal stability of two beetle populations in non-farmed habitats in an agricultural landscape. *J. Appl. Ecol.* 43, 680–689.
- Camara, K.M., Payne, W.A., Rasmussen, P.E., 2003. Long-term effects of tillage, nitrogen, and rainfall on winter wheat yields in the Pacific Northwest. *Agron. J.* 95, 828–835.

- Cherry, R., Stansly, P., 2008. Abundance and spatial distribution of wireworms (Coleoptera: Elateridae) in Florida sugarcane fields on muck versus sandy soils. *Fla. Entomol.* 91, 383–387.
- Comstock, J.H., Slingerland, M.V., 1891. Wireworms, vol. 33. Cornell University, Ithaca, New York.
- Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466, 109–112.
- Doane, J.F., Klingler, J., 1978. Location of CO₂-receptive sensilla on larvae of the wireworms *Agriotes lineatus-obscurus* and *Limonium californicus*. *Ann. Entomol. Soc. Am.* 71, 357–363.
- Doane, J.F., Lee, Y.W., Klingler, J., Westcott, N.D., 1975. The orientation response of *Ctenicera destructor* and other wire worms (Coleoptera: Elateridae) to germinating grain and to carbon dioxide. *Can. Entomol.* 107, 1233–1252.
- Ehrlén, J., Morris, W.F., 2015. Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* 18, 303–314.
- Esser, A.D., Milosavljević, I., Crowder, D.W., 2015. Effects of neonicotinoids and crop rotation for managing wireworms in wheat crops. *J. Econ. Entomol.* 108, 1786–1794.
- Etzler, F.E., Wanner, K.W., Morales-Rodriguez, A., Ivie, M.A., 2014. DNA barcoding to improve the species-level management of wireworms (Coleoptera: Elateridae). *J. Econ. Entomol.* 107, 1476–1485.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotech.* 3, 294–299.
- Furlan, L., Kreutzweiser, D., 2015. Alternatives to neonicotinoid insecticides for pest control: case studies in agriculture and forestry. *Environ. Sci. Pollut. R.* 22, 135–147.
- Furlan, L., 2004. The biology of *Agriotes sordidus* Illiger (Col., Elateridae). *J. Appl. Entomol.* 128, 696–706.
- Furlan, L., 2014. IPM thresholds for *Agriotes* wireworm species in maize in Southern Europe. *J. Pest. Sci.* 87, 609–617.
- Gibson, K.E., 1939. Wireworm damage to potatoes in the Yakima Valley of Washington. *J. Econ. Entomol.* 32, 122–124.
- Glen, R., King, K.M., Arnason, A.P., 1943. The identification of wireworms of economic importance in Canada. *Can. J. Res.* 21, 358–387.
- Glen, R., 1950. Larvae of the elaterid beetles of the tribe Lepturodini (Coleoptera: Elateridae). *Smithson. Misc. Collect.* 11, 1–246.
- Gui, H.L., 1935. Soil types as factors in wireworm distribution. *Am. Potato J.* 12, 107–113.
- Hermann, A., Brunner, N., Hann, P., Wrba, T., Kromp, B., 2013. Correlations between wireworm damages in potato fields and landscape structure at different scales. *J. Pest. Sci.* 86, 41–51.
- Higginbotham, R.W., Froese, P.S., Carter, A.H., 2014. Tolerance of wheat (Poales: Poaceae) seedlings to wireworm (Coleoptera: Elateridae). *J. Econ. Entomol.* 107, 833–837.
- Horton, D.R., Landolt, P.J., 2002. Orientation response of Pacific coast wireworm (Coleoptera: Elateridae) to food baits in laboratory and effectiveness of baits in field. *Can. Entomol.* 134, 357–367.
- Horton, D.R., 2006. Quantitative relationship between potato tuber damage and counts of Pacific coast wireworm (Coleoptera: Elateridae) in baits: seasonal effects. *J. Entomol. Soc. B. C.* 103, 37–48.
- Huggins, D.R., Reganold, J.P., 2008. No-till: the quiet revolution. *Sci. Am.* 299, 70.
- Ibrahim, H.M., Huggins, D.R., 2011. Spatio-temporal patterns of soil water storage under dryland agriculture at the watershed scale. *J. Hydrol.* 404, 186–197.
- Johnson, S.N., Nielsen, U.N., 2012. Foraging in the dark—chemically mediated host plant location by belowground insect herbivores. *J. Chem. Ecol.* 38, 604–614.
- Jones, E.W., Shirck, F.H., 1942. The seasonal vertical distribution of wireworms in the soil in relation to their control in the Pacific Northwest. *J. Agric. Res.* 65, 125–142.
- Jung, J., Racca, P., Schmitt, J., Kleinhenz, B., 2014. SIMAGRIO-W: development of a prediction model for wireworms in relation to soil moisture, temperature and type. *J. Appl. Entomol.* 138, 183–194.
- Keiser, A., Häberli, M., Stamp, P., 2012. Quality deficiencies on potato (*Solanum tuberosum* L.) tubers caused by *Rhizoctonia solani*, wireworms (*Agriotes* spp.) and slugs (*Deroceras reticulatum*, *Arion hortensis*) in different farming systems. *Field Crop Res.* 128, 147–155.
- Koenig, R., Schroeder, K., Carter, A., Pumphrey, M., Paulitz, T., Campbell, K., Huggins, D., 2011. Soil Acidity and Aluminum Toxicity in the Palouse Region of the Pacific Northwest. Washington State University Fact Sheet FS050E, Washington State University Extension, Pullman, WA.
- Kovács, T., Kuroli, G., Pomsár, P., Németh, L., Páli, O., Kuroli, M., 2006. Localisation and seasonal positions of wireworms in soils. *Commun. Agric. Appl. Biol. Sci.* 71, 357–367.
- Kutner, M.H., Nachtsheim, C.J., Neter, J., Li, W., 2005. Applied Linear Statistical Models. McGraw-Hill/Irwin.
- Lanchester, H.P., 1946. Larval determination of six economic species of *Limonium* (Coleoptera: Elateridae). *Ann. Entomol. Soc. Am.* 39, 619–626.
- Lane, M.C., 1925. The economic wireworms of the Pacific Northwest (Elateridae). *J. Econ. Entomol.* 18, 90–95.
- Lefko, S.A., Pedigo, L.P., Batchelor, W.D., Rice, M.E., 1998. Spatial modeling of preferred wireworm (Coleoptera: Elateridae) habitat. *Environ. Entomol.* 27, 184–190.
- Lindroth, E., Clark, T.L., 2009. Phylogenetic analysis of an economically important species complex of wireworms (Coleoptera: Elateridae) in the Midwest. *J. Econ. Entomol.* 102, 743–749.
- Majka, C.G., Johnson, P.J., 2008. The Elateridae (Coleoptera) of the Maritime Provinces of Canada: taxonomic changes, new records, faunal composition, collecting history and zoogeography. *Zootaxa* 1811, 1–33.
- Marske, K.A., Ivie, M.A., 2003. Beetle fauna of the United States and Canada. *Coleopt. Bull.* 57, 495–503.
- Milosavljević, I., Esser, A.D., Crowder, D.W., 2016. Seasonal population dynamics of wireworms in wheat crops in the Pacific Northwestern United States. *J. Pest. Sci.* doi:10.1007/s10340-016-0750-y.
- Parker, W.E., Howard, J.J., 2001. The biology and management of wireworms (*Agriotes* spp.) on potato with particular reference to the UK. *Agric. For. Entomol.* 3, 85–98.
- Parker, W.E., Seeney, F.M., 1997. An investigation into the use of multiple site characteristics to predict the presence and infestation level of wireworms (*Agriotes* spp., Coleoptera: Elateridae) in individual grass fields. *Ann. Appl. Biol.* 130, 409–425.
- Pedigo, L.P., Rice, M., 2008. Entomology and Pest Management, sixth ed. Prentice Hall, Upper Saddle River, NJ.
- Price, P.W., Denno, R.F., Eubanks, M.D., Finke, D.L., Kaplan, I., 2012. Insect Ecology: Behavior, Populations and Communities. Cambridge University Press, New York.
- Qiu, H., Huggins, D.R., Wu, J.Q., Barber, M.E., McCool, D.K., Dun, S., 2011. Residue management impacts on field-scale snow distribution and soil water storage. *Trans. ASABE* 54, 1639–1647.
- Reddy, G.V.P., Tangtrakulwanich, K., Wu, S., Miller, J.H., Ophus, V.L., Prewett, J., Jaronski, S.T., 2014. Evaluation of the effectiveness of entomopathogens for the management of wireworms (Coleoptera: Elateridae) on spring wheat. *J. Invertebr. Pathol.* 120, 43–49.
- SAS Institute, 2012. SAS/STAT, Version 9.2 User's Guide, 2nd ed. SAS Institute, Cary, NC.
- Schaetzl, R., Anderson, S., 2005. Soils: Genesis and Geomorphology, 1st ed. Cambridge University Press, New York, NY.
- Schillinger, W.F., Papendick, R.I., 2008. Then and now: 125 years of dryland wheat farming in the Inland Pacific Northwest. *Agron. J.* 100, 166–182.
- Schillinger, W.F., Papendick, R.I., Guy, S.O., Rasmussen, P.E., van Kessel, C., 2006. Dryland cropping in the western United States. In: Peterson, G.A., Unger, P.W., Payne, W.A. (Eds.), Dryland Agriculture. 2nd ed. Agronomy Monograph no 23. ASA, CSSA, and SSSA, Madison, WI, pp. 365–393.
- Shirck, F.H., 1945. Crop rotations and cultural practices as related to wireworm control in Idaho. *J. Econ. Entomol.* 38, 627–633.
- Smith, K.A., Mullins, C.E., 1991. Soil Analysis. Physical Methods. Marcel Dekker, New York.
- Staudacher, K., Pitterl, P., Furlan, L., Cate, P.C., Traugott, M., 2011. PCR-based species identification of *Agriotes* larvae. *Bull. Entomol. Res.* 101, 201–210.
- Staudacher, K., Schallhart, N., Pitterl, P., Wallinger, C., Brunner, N., Land, M., Kromp, B., Glauning, J., Traugott, M., 2013. Occurrence of *Agriotes* wireworms in Austrian agricultural land. *J. Pest. Sci.* 86, 33–39.
- Taubner, H., Roth, B., Tippkötter, R., 2009. Determination of soil texture: comparison of the sedimentation method and the laser-diffraction analysis. *J. Plant Nutr. Soil Sci.* 172, 161–171.
- Thomas, C.A., 1940. The biology and control of wireworms: a review of the literature. *Bull. Pa. Agric. Exp. Stn.* 392, 1–90.
- Toba, H.H., Campbell, J.D., 1992. Wireworm (Coleoptera: Elateridae) survey in wheat-growing areas of northcentral and northeastern Oregon. *J. Entomol. Soc. B. C.* 89, 25–30.
- Toba, H.H., Turner, J.E., 1983. Evaluation of baiting techniques for sampling wireworms (Coleoptera: Elateridae) infesting wheat in Washington. *J. Econ. Entomol.* 76, 850–855.
- Toepfer, S., Ellsbury, M.M., Eschen, R., Kuhlmann, U., 2007. Spatial clustering of *Diabrotica virgifera virgifera* and *Agriotes ustulatus* in small-scale maize fields without topographic relief drift. *Entomol. Exp. Appl.* 124, 61–75.
- Traugott, M., Schallhart, N., Kaufmann, R., Juen, A., 2008. The feeding ecology of elaterid larvae in central European arable land: new perspectives based on naturally occurring stable isotopes. *Soil Biol. Biochem.* 40, 342–349.
- Traugott, M., Benefer, C.M., Blackshaw, R.P., van Herk, W.G., Vernon, R.S., 2015. Biology, ecology, and control of Elaterid Beetles in agricultural land. *Annu. Rev. Entomol.* 60, 313–334.
- Vernon, R.S., van Herk, W.G., Tolman, J., Saavedra, H.O., Clodius, M., Gage, B., 2008. Transitional sublethal and lethal effects of insecticides following dermal exposures to five economic species of wireworms (Coleoptera: Elateridae). *J. Econ. Entomol.* 101, 367–374.
- Vernon, R.S., van Herk, W.G., Clodius, M., Harding, C., 2009. Wireworm management I: stand protection versus wireworm mortality with wheat seed treatments. *J. Econ. Entomol.* 102, 2126–2136.
- Villani, M.G., Wright, R.J., 1990. Environmental influences on soil macroarthropod behavior in agricultural systems. *Annu. Rev. Entomol.* 35, 249–269.
- Whittingham, M.J., Stephens, P.A., Bradbury, R.B., Freckleton, R.P., 2006. Why do we still use stepwise modeling in ecology and behaviour? *J. Anim. Ecol.* 75, 1182–1189.
- van Herk, W.G., Vernon, R.S., 2007. Soil bioassay for studying behavioral responses of wireworms (Coleoptera: Elateridae) to insecticide-treated wheat seed. *Environ. Entomol.* 36, 1441–1449.
- Willis, R.B., Abney, M.R., Holmes, G.J., Schultheis, J.R., Kennedy, G.G., 2010. Influence of preceding crop on wireworm (Coleoptera: Elateridae) abundance in the coastal plain of North Carolina. *J. Econ. Entomol.* 103, 2087–2093.