Soil Invertebrate Community Response to Climate Patterns in a South-Central Oklahoma Grassland

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Abstract: Soil invertebrates are an important, but often overlooked, component of the soil ecosystem. In temperate grassland, they are involved in nutrient cycling, breakdown of detritus, and soil fertility. Soil invertebrate populations are affected by the quality of detritus in the soil; there is evidence that both grazing and fire can increase invertebrate populations by improving the quality of litter in soil. It is also possible their population sizes are affected by climatic conditions. I surveyed a degraded grassland site over six years and quantified invertebrate populations (by order) in the top 8 cm of soil. During the years of this survey, a serious drought (2011) took place, which apparently affected invertebrate diversity. Over the years of the study, Shannon diversity decreased but number of invertebrates increased. That increase appears to be the result of increases in the Acarina, Collembola, and the ants (specifically, red imported fire ants). Management recommendations for the site include either burning or grazing to remove accumulated fuel, and removal of invading woody plants.

Introduction

Soil invertebrates, primarily in Phyla Annelida, Aschelminthes, and Arthropoda, play many vital roles in soil ecosystems. They are involved in breakdown of detritus and nutrient cycling (Davis et al 2006, Seastedt 2000). They can improve soil fertility and structure and can alter primary production (Davis et al. 2006). The soil presents a complete ecosystem and a complex food web (Seastedt 1984). However, because of the small size and inconspicuous location of soil invertebrates, they are relatively little-known, and their effects on decomposition rates are not widely studied (Wall et al. 2008). Seastedt (2000) notes that soil invertebrates may control certain ecosystem processes, but this fact may be "opaque" to many researchers in ecosystems or soils, because often the contributions of the invertebrates are summarized in proxy variables that are easier to measure. Additionally, identifying individual species of some groups is very challenging (e.g., Aschelminthes must be identified based on mouthpart anatomy).

Soil invertebrates are particularly involved in nutrient cycling in prairie communities; Tscharntke and Greiler (1995) suggest that the soil invertebrate community consumes two to ten times the amount of standing crop in the soil that aboveground herbivores do. In tallgrass prairie, the soil fauna can be particularly diverse: Seastedt et al. (1988) note that there is a great deal of root turnover in the tallgrass prairie, leading to a buildup of organic matter. This leads to a soil fauna that is "diverse and abundant," according to them. Additionally, within different types of grassland, there is considerable variation as to what group of soil invertebrates is dominant (Seastedt 2000). Just as communities vary

by location, because locations differ in abiotic factors like temperature and moisture availability, so could the community at a single site vary over time with fluctuations in climate or other environmental factors.

Soil invertebrates can be affected by fire (Seastedt et al. 1988), seasonal changes in soil temperature profile (Dowdy 1944), grazing or mowing (Seastedt and Reddy 1991), and vegetational changes. Any factor that affects root productivity can affect soil invertebrate populations. Some soil invertebrate populations show wide short-term fluctuation without large effects on long-term population dynamics (Brand 2002). These populations are often referred to as "resilient" – that is, able to rebound following disturbance (Wall et al 2008). There are few recent studies of soil invertebrate population change, in particular as a result of drought. Because the soil invertebrate community tends to vary from season to season and year to year, single samples do not give a complete picture of the diversity of soil invertebrates at a site. There are some historical papers that address seasonal and yearly patterns of change (Dowdy 1944, Shackleford 1942), but few more recent studies. With long-term climate change patterns, including an increased risk of drought in Western states, understanding its effects on soil detritivores and soil invertebrates in general will be important.

The data reported in the current study were collected to develop a baseline of soil-invertebrate order abundance and diversity during prairie restoration of formerly grazed land. The aim was to determine if, and how, the community of invertebrates changed as vegetation changed. Initial results of these data (using a slightly different method of classifying organisms; I used a simplified classification, going only to order level, in this paper) were previously published by Corbett (2012).

To examine changes in abundance and diversity of soil invertebrate populations over time, I tested for patterns over the seasons and years of this study, and compared these patterns to patterns in climate. Dowdy (1944) proposed that soil invertebrates move up and down in the soil column over the course of the year, as the "temperature turnover" happens in the soil from fall to spring. In addition, as site conditions like vegetation heterogeneity or moisture availability change over the longer term, soil-invertebrate community structure can change and undergo a sort of succession (Jonas et al 2002). In particular, I examined the relationship between certain community parameters (number of organisms, number of orders represented, Shannon diversity) and environmental factors (in particular, rainfall and temperature). I also examined the most abundant taxa for changes in population size over time.

Methods

The field site is formerly-grazed land near Roberta, Oklahoma (N335230, W 0961500 – see Figure 1). The site is considered an upland site and has a homogenous soil association throughout (Crockett-Durant complex: USDA, 1978). The site has been free of grazing since 2001. In 2004, a colleague (Tim Patton) and I began a process of prairie restoration on the site. For sampling purposes, forty 10m x 10m blocks were laid out and were marked in their northwest corner with metal poles so that the sites could be relocated (see figure 2). The blocks were arranged in five rows of eight each. Vegetation on the site was a mixture of native grassland species and introduced pasture species. Dominant species of grasses include several species of bluestems (*Andropogon spp.* and *Schizachyrium scoparius*). Three-awn grass (*Aristida oligantha*), sand lovegrass (*Eragrostis trichoides*) and Scribner's panic grass (*Panicum oligosanthes*) are also present. The dominant forbs include several species of aster (primarily heath aster, *Aster ericoides)*, Iva (*Iva annua*) and goldenrod (most likely *Solidago gigantea*). Blackberry (*Rubus oklahomus*) is also present. (All nomenclature follows Noble Foundation's Plant Image Gallery, http://www.noble.org/Apps/PlantImageGallery/index.aspx). In 2006, some of the blocks were raked and overseeded with a prairie mix.

I began sampling the site for soil

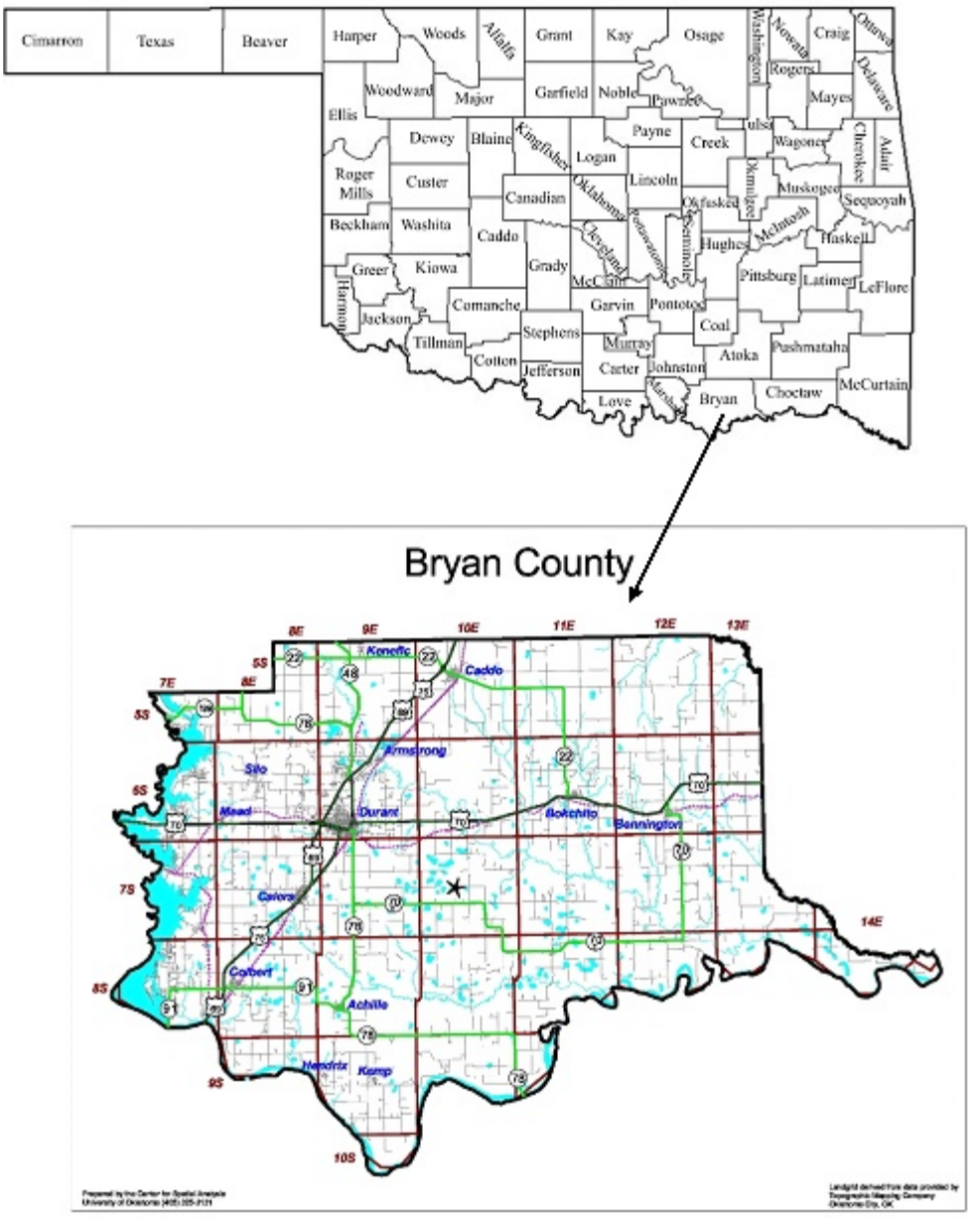

Figure 1: Location of sample site in Bryan County, Oklahoma. Approximate location of sample site is shown with a star.

invertebrates in early spring 2009. Three samples per year were taken: early March, early June, and early October. Twenty of the forty blocks (see Figure 2) were sampled, following a "staggered" pattern (e.g., blocks 1, 3, 5, and 7 in the first row, and 10, 12, 14, and 16 in the second row). Five soil samples were collected per block sampled, 6.5 cm in diameter by 5 cm deep. A standard bulb planter ("Garden Plus 5 inch steel bulb planter," Lowe's) was used to collect the samples. Each block's samples were placed in a zipper-top bag and were

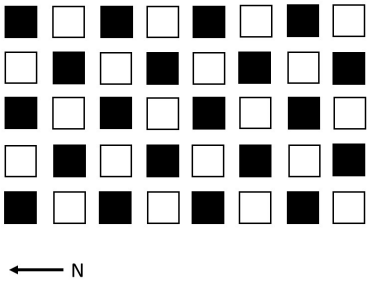

Figure 2: Diagram showing sample site. Filled-in blocks represent blocks sampled in this study. Block size is 10 m x 10m

kept in a cooler at ~ 20° C until transported to Southeastern Oklahoma State University.

Soil invertebrates were extracted from the soil using a combination of a modified Berlese funnel method and a floatation method. For the funnel extraction, heavy foil 2-quart aluminum casserole pans (Hefty EZ Foil) and plastic needlepoint mesh with 1 mm holes (e.g., JoAnn Fabric and Crafts) was used. Most of the bottom of each pan was cut out and replaced with a slightly larger circle of the needlepoint mesh. These "funnels" were then set on top of 1000 mL beakers containing about 20 mL of 70% isopropyl alcohol as a preservative. Soil samples were placed in the casserole pan and a 25 watt light bulb shone on the surface of the soil for 24 hours. (A low-wattage light bulb was used because the rooms were unattended during the time of extraction). After extraction, the alcohol and any invertebrates in it were transferred to 120-mL plastic specimen cups for storage. Additionally, the remaining soil in the funnel was searched using a "floatation" technique to find and extract invertebrates that did not travel through the holes in the mesh. In some cases, this was because they were too large (beetles and larger isopods); in other cases, they did not travel far enough down through the soil. Each soil sample was split into smaller portions (to scarcely fill the bottom of a 150 mm petri dish), wetted excessively, and examined under 20X magnification using a dissecting microscope. Any invertebrates observed were removed using a dissecting needle or forceps and placed in the appropriate sample's vial.

After completing the full extraction procedure, I examined the contents of each vial. Again, I examined the organisms using a dissecting microscope on 20X magnification. A red filter (a sheet of translucent plastic placed over the baseplate) was used to make the organisms easier to see (and to reduce eyestrain). Samples were broken down into 4-5 mL aliquots to make examination easier. Each aliquot was examined and individual invertebrates were identified to order and counted. The "Kwik-key to soil invertebrates" (Meyer, 1994) was used to assist with identification. In most cases, organisms were separated to order or class; in a few cases (like Aschelminthes) where that type of separation was difficult, identification was left at the phylum level. However, the identification scheme used was consistent across all samples, so relative comparisons of numbers and diversity should be valid. In general, the identification scheme was similar to that used by Wall et al. (2008).

Data were analyzed using Shannon diversity indexes (Magurran, 1988). Base-ten logarithms were used in the calculation of the Shannon index. Evenness was also calculated for each sample. In addition, I analyzed samples based on total number of organisms present and on number of orders represented in the sample (order richness). Statistical analyses were performed using IBM SPSS version 20 (IBM, 2013). Initially, data were analyzed using a non-parametric analogue of Analysis of Variance (Kruskal-Wallis). Two sets of analyses were performed: using season (spring, summer, fall) as the grouping variable or using year (2009-2014) as the grouping variable. The dependent variables included Shannon diversity, evenness, number of soil invertebrates, and number of orders represented in the sample. There were insufficient degrees of freedom to run a two-way GLM analysis to examine the interaction term, so simple one-way analysis was used.

Because the samples were small and generally did not fulfill the assumption of

Table 1: Temperature data for South-Central Oklahoma during the period of the soil-invertebrate study. "Average temperature" is the average temperature for the entire year. "Previous month" is the average temperature for the month prior to the sample. "Current Month" is the temperature for the month of the sample.

Sample period	Average temperature	Previous month	Current Month
March 2009	16.6° C	10.6° C	13.2° C
June 2009	16.6° C	19.8° C	26.9° C
October 2009	16.6° C	22.2° C	14.2° C
March 2010	16.9° C	3.5° C	10.72° C
June 2010	16.9° C	21.5° C	28.0° C
October 2010	16.9° C	24.7° C	17.3° C
March 2011	17.8° C	6.2° C	13.6° C
June 2011	17.8° C	20.4° C	29.3° C
October 2011	17.8° C	23.1° C	17.7° C
March 2012	18.3° C	8.5° C	16.5° C
June 2012	18.3° C	23.1° C	26.3° C
October 2012	18.3° C	24.6° C	16.3° C
March 2013	16.2° C	7.7° C	10.3° C
June 2013	16.2° C	20.2° C	26.1° C
October 2013	16.2° C	25.7° C	17.7° C
March 2014	16.2° C	4.0° C	9.3° C
June 2014	16.2° C	21.1° C	26.0° C
October 2014	16.2° C	24.0° C	19.5° C

Table 2: Precipitation data for South-Central Oklahoma during the period of the soil-invertebrate study. "Annual precipitation" is the total precipitation for the entire year. "Previous month" is the total precipitation for the month prior to the sample. "Current Month" is the total precipitation for the month of the sample.

Sample period	Annual precipitation	Previous month	Current Month
March 2009	119.5 cm	3.5 cm	5.5 cm
June 2009	119.5 cm	20.2 cm	8.2 cm
October 2009	119.5 cm	13.0 cm	24.8 cm
March 2010	87.8 cm	7.5 cm	6.4 cm
June 2010	87.8 cm	11.9 cm	9.3 cm
October 2010	87.8 cm	16.2 cm	4.9 cm
March 2011	61.5 cm	4.3 cm	0.7 cm
June 2011	61.5 cm	14.5 cm	0.9 cm
October 2011	61.5 cm	3.7 cm	9.8 cm
March 2012	74.3 cm	3.7 cm	13.7 cm
June 2012	74.3 cm	6.9 cm	7.8 cm
October 2012	74.3 cm	8.5 cm	9.8 cm
March 2013	96.9 cm	7.7 cm	4.6 cm
June 2013	96.9 cm	18.1 cm	11.8 cm
October 2013	96.9 cm	4.8 cm	9.9 cm
March 2014	81.8 cm	1.5 cm	6.2 cm
June 2014	81.8 cm	6.4 cm	14.6 cm
October 2014	81.8 cm	5.9 cm	7.9 cm

Table 3: Most abundant taxa by sampling period, with number of individuals observed.

Year	March		June		October	
2009	Protura	68	Diplura	130	Protura	47
	Acarina	35	Hymenoptera	76	Acarina	43
	Collembola	23	Acarina	56	Hymenoptera	21
					Annelida	31
2010	Protura	49	Acarina	213	Acarina	103
	Annelida	36	Collembola	96	Hymenoptera	84
	Acarina	22	Hymenoptera	48	Collembola	56
2011	Hymenoptera	203	Hymenoptera	192	Acarina	59
	Acarina	99	Acarina	117	Hymenoptera	26
	Collembola	59	Collembola	34	Coleoptera	19
	Protura	53	Coleoptera	32		
2012	Collembola	212	Acarina	316	Acarina	292
	Hymenoptera	63	Collembola	222	Collembola	123
	Acarina	55	Hymenoptera	115	Hymenoptera	101
2013	Acarina	269	Acarina	172	Acarina	188
	Collembola	155	Collembola	126	Hymenoptera	97
	Diplura	25	Hymenoptera	110	Collembola	65
2014	Hymenoptera	181	Hymenoptera	533	Hymenoptera	292
	Acarina	159	Acarina	250	Acarina	204
	Collembola1	29	Collembola	50	Collembola	103

equal variances, they were analyzed using non-parametric methods. However, because of a lack of follow-up tests for the nonparametric analyses, the significant analyses were tested parametrically using REGWQ: the Ryan-Einot-Gabriel-Welch q test: a modification of the t test used as a follow up after analyses of variance (IBM, 2013) to determine which groups differed.

Additionally, Pearson correlations were run on pairs of variables to look for trends. I compared year, season, and number of the sample (1 through 18: eighteen samples were collected over the course of this study) against diversity and abundance to determine if there were any temporal or seasonal patterns.

To analyze the data in greater detail, I obtained climate data for the South Central Oklahoma region (Climate Region 8 on http://www.ncdc.noaa.gov/cag/time-series/us). First, I obtained annual rainfall totals for the years 2009 through 2014, and average annual temperatures (see table 1). In addition, I compiled data on monthly precipitation (table 2) and monthly temperatures (table 1) for the month of the sampling and the month immediately previous to it. Samples were typically collected early in the month, so it is assumed the previous month's conditions could have an effect. Again, Pearson correlations were run to determine possible relationships between variables.

Results

Over the course of the study, the "majority" taxa (those with the greatest number of individuals) were fairly consistent (see table 3). Generally, mites and springtails showed high abundance throughout the study. Numbers seemed to increase post-2011, perhaps as a result of the drought that year. Over time, diversity decreased but number of individuals in the samples increased; that increase may be linked to these three taxa increasing over time.

Analysis for year effect and for season effect using Kruskal-Wallis analysis revealed only one significant result: that of year on diversity. The p value of this test (SPSS does not provide the value of the Kruskal-Wallis test statistic) was 0.038. None of the other comparisons against year (of evenness, of order richness, of total number of invertebrates) showed significance, and none of the comparisons against season was significant. There was considerable variation from year-to-year within a single season.

Comparing individual years more closely, years 2009, 2010, and 2011 were not significantly different in their diversity. Years 2010-2014 were also not significantly different in their diversity. However, year 2009 was significantly more diverse than years 2012-2014. There is a trend of a decline in diversity following 2011. In southern Oklahoma, 2011 was a severe drought year, with 34.8 cm less rainfall than average. (National Climate Data Center).

Correlation analysis revealed additional patterns. There were significant correlations between year of sampling and diversity ($p<0.001$, $n=15$, correlation coefficient -0.796). Diversity declined with year of sampling, which agrees with the Kruskal-Wallis analysis. There was also a significant correlation between year and number of organisms ($p=0.035$, $n=15$, correlation coefficient = 0.546). As time passed, there was a trend toward decreasing diversity but increasing number of organisms. Season showed no significant correlation with any of the other variables.

Comparing the most abundant taxa against year, season, and "sample order" (where the first sample in spring 2009 was 1 and the sample in fall 2014 was number 18) revealed a few patterns. Three groups showed a significant increase over the years of the study (Collembola: $p=0.004$, correlation coefficient = 0.643; Isopoda: $p=0.021$ correlation coefficient=0.541; Acarina: $p=0.004$, correlation coefficient=0.643). Only one group, Isopoda, showed a relationship with season ($p=0.026$, correlation coefficient=0.522), demonstrating that the number of isopods tended to increase later in the year. For "sample number," again Collembolans, Isopoda, and Acarina showed significant correlations, but ants also showed a marginally significant

(p=0.50, correlation coefficient = 0.468) correlation. These groups apparently increased over the period of sampling of this site.

Climatological patterns, beyond mere seasonal differences, can have an effect on soil invertebrates (McLean et al, 1977. Jonas et al 2002). There was variation in precipitation (see table 2) across the years of the study. There was also variation in temperature, both in terms of average annual temperature and in temperature of the months surrounding the sampling times (see table 1 for temperature data). Monthly temperatures showed no significant correlations with any of the community variables, but there was a significant correlation between average annual temperature and number of orders present (coefficient =-0.489, p=0.039). In warmer years, the number of orders appearing in samples declined. Similarly, there were no patterns related to monthly rainfall amounts, but total annual precipitation was correlated with diversity (coefficient = 0.524, p=0.026). As total precipitation in a year increased, diversity also increased.

Individual taxa showed relatively few patterns in response to environmental variables. Phylum Annelida decreased in abundance with increasing annual temperature (p=0.037, correlation coefficient = -0.494) and decreased with increasing previous month's temperature (p=0.025, coefficient=-0.520). Springtails (Order Collembola, Phylum Arthropoda) decreased with increasing annual precipitation (p=0.044, correlation coefficient =-0.480). Isopods (Order Isopoda, Phylum Arthropoda) showed an increase in abundance with increasing temperatures in the previous month (p=0.014, correlation coefficient= 0.568).

Discussion

Kruskal-Wallis analysis of year and season effects on diversity, evenness, order richness, and total number of organisms revealed a significant effect of year on diversity. Diversity declined over the course of the study, with the first year showing high diversity, and years 2012-2014 being significantly lower in diversity. It is notable that 2011 was an extreme drought year for southern Oklahoma, with almost 35 cm of precipitation less than average (roughly 96 cm). The year 2012 was also droughty, with 22 cm less precipitation than the average (National Climate Data Center). Seasons showed no pattern as far as diversity, evenness, or numbers of taxa/numbers of organisms were concerned.

The year 2011 was a serious drought year that apparently had an effect on species diversity (2012 had the lowest average diversity). Different taxa are affected to different degrees by drought; in a study in wet meadows, Davis et al (2006) noted a decline in earthworm and scarab beetle populations in drought years, but an increase in Isopoda. Whether the declines observed are actual declines, or merely evidence of the invertebrates moving deeper into the soil column is unclear, but perhaps the effect on upper-horizon decomposition and nutrient cycling would be similar in either case.

The two main patterns over the sampling period are a decrease in diversity after the drought of 2011, and an increase in total number of organisms over time. The trend of increasing numbers of organisms over time is more difficult to explain; few manipulations have been done to the site since it was abandoned from grazing in 1980. The increase may be the result of gains in numbers, at least for some sampling periods, in ants, mites, and collembolans. While overall diversity tended to decline, a few taxonomic groups became more abundant, which would, itself, have reduced diversity. Dowdy (1965) states that "moisture does not appear to be a factor" in the abundance and diversity of mites and collembolans; perhaps they are less affected by these kinds of environmental fluctuations than some other groups, and they were able to take advantage of reduced competition following the dry period of 2011-2012.

Examining individual orders of invertebrates and their abundance, in general the same few groups showed highest abundance in each sample. Mites (order Acarina) were in the top three groups (in terms of abundance) in every sampling period. (see table 3). Springtails

(Order Collembola) were the most abundant order in 13 of the 16 samples. Other highly abundant groups included beetles (Coleoptera), earthworms (Phylum Annelida), and ants (order Hymenoptera). Maclean et al. (1977), in their study in Alaska, determined that mites and springtails were the most abundant groups present in their soils. The abundance of mites and collembolans should not be surprising; Seastedt (1984) noted that they comprise roughly 95% of arthropods found in grassland ecosystesm.

Some types of habitat loss or fragmentation may affect invertebrates strongly without showing large effects on vertebrate animals. This is especially true of small-scale or short-duration disturbances (Jonas et al., 2002). Even though soil organisms are often considered to have population "resiliency" (where they can rebound rapidly after a disturbance), prolonged or multiple disturbances could alter community make-up over time. Disturbances can alter soil moisture, organic matter, root biomass, and soil chemistry, all factors that could affect invertebrate populations (Davis et al 2006). Wall et al (2008) suggest that actual taxonomic diversity of soil organisms may be as important to decomposition rates as sheer number of organisms – and therefore any long-term loss of diversity could alter decomposition and nutrient-cycling patterns at a site. Chemical pollution, overuse of pesticides, extended drought, or other climate changes could alter the soil community and as a result alter decomposition rates, litter accumulation, and nutrient dynamics at a site.

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