Interaction responses between *Folsomia quadrioculata* and *Folsomia manolachei* in two types of soil and at different temperatures

Master thesis in ecology, 2009

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CONTENTS

ABSTRACT

The interactions between *Folsomia quadrioculata* and *Folsomia manolachei* and their body growth rates were investigated in grey-brown podzolic soil and in raw humus from podzol at 10^{o}C and 20^{o}C**.** *F. quadrioculata* did best in raw humus, at both temperatures, when they were in one-species boxes; however, *F. quadrioculata* also did better than *F. manolachei* in one-species boxes with mold at 10^{o}C, which was not expected. *F. quadrioculata* also has a negative effect on *F. manolachei* when they are in interaction boxes with mold, so *F. manolachei* have a higher number of individuals in one-species boxes than in interaction boxes with mold. On the other hand, *F. manolachei* has a negative effect on *F. quadrioculata* when they are in interaction boxes with raw humus, so *F. quadrioculata* has a higher number of individuals in one-species boxes compared to interaction boxes when they are in raw humus. The temperature does not have an effect on the outcomes of the different tests, *F. quadrioculata* did better in one-species boxes than in interaction boxes with raw humus, at both temperatures, and *F. manolachei* did better in one-species boxes than in interaction boxes with mold, at both temperatures, with one exception: *F. quadrioculata* does better than *F. manolachei* in one-species boxes with mold at 10^{o}C and *F. manolachei* does better than *F. quadrioculata* in one-species boxes at 20^{o}C. However, statistical analyses show that soil and temperature have significant effects on the populations. Soil type also has a significant effect on the growth rate for *F. manolachei* at 4 weeks, and at 8 weeks both soil and temperature have significant effects on the growth rate for *F. manolachei*. While the growth rate of *F. quadrioculata* is significantly influenced by both soil and temperature at 4 weeks, and soil significantly effects growth rate at 8 weeks.

INTRODUCTION

Collembola, also known as spring tails, is an order of hexapod arthropods. The taxonomic placement of Collembola has been controversial for a long time but the latest census is that Collembola is an order, Order Collembola, in Noninsectan Hexapods (Hickman 2006). Due to the small size of Collembola (usually 0.5–2 mm) they are categorized as microarthropods. Together with mites, the Collembola is by far the most abundant and widespread group among the soil microarthropods (Hopkin 1997, Rusek 1998).

Collembola have been present on Earth for more than 400 million years, which makes them part of the earliest colonizing arthropods (Hopkin 1997). Most Collembola species live in the soil environment where they are among the most abundant and widespread groups of arthropods, and they can be found everywhere in the world, on every continent (Hopkin 1997). Collembola is numerous in all forest soils in Norway, usually in the order of 10^4-10^5 ind.m^{-2}, and particularly so in coniferous forest with raw humus where they frequently reach densities up to 100,000 - 200,000 ind.m^{-2} (Hagvar 1982, Leinaas 1978a) (H.P.Leinaas personal communication). A high number of collembolan species can be found within small areas (<m^2), but with only moderate change in species composition across different habitats and areas (Hagvar 1982, H.P.Leinaas personal communication). Thus, the Collembola appears to have a relatively high alpha-diversity and low beta diversity. Nevertheless, the soil ecosystem is characterized by high species diversity.

The food web below ground in temperate ecosystems contains a diverse community consisting of microbes, fungi, and animals that may interact in “symbiotic, commensal, and predatory manners simultaneously” (Harris and Boerner 1990). The majority of nutrient mineralization is done by bacteria and fungi. However, Collembola and other microarthropods influences the bacteria and fungi’s ability to perform their tasks (Cragg and Bardgett 2001). Most Collembola species belong to the decomposer trophic level (Addison and Parkinson 1978), and due to their importance in the soil system, they may have a significant function in “decomposition and nutrient cycling in forest ecosystems” (Hasegawa, Fukuyama, Makino, Okochi, Goto, Mizoguchi, Sakata and Tanaka 2006). The Collembola communities are influenced by several factors, including soil fertility, humus type, and water content (Hasegawa, Fukuyama, Makino, Okochi, Goto, Mizoguchi, Sakata and Tanaka 2006).

Most species of Collembola have been categorized as fungivores or detritivores. However, studies have shown that many of these species in fact are generalist that feed on a wide range of microorganisms (Jensen, Leinaas and Hessen 2006, Sadaka-Laulan and Ponge 2000) including fungi, algae, cyanobacteria, and bacteria (Gange 2000, Scheu and Simmerling 2004), with a tendency to prefer fungal hyphae (Hopkin 1997). By grazing on fungi, Collembola stimulates the fungi to grow and respire, and thereby enhance the decomposition process (Larsen, Johansen, Erik Larsen, Henrik Heckmann, Jakobsen and Henning Krogh 2008). The different species influences the decomposition process through their feeding activities and transportation of fungal propagules (Chauvat, Zaitsev and Wolters 2003, Seastedt 1984). When Collembola consumes dead vegetation the surface area is increased which makes it more suitable for attacks from fungi and other microbes. Collembola also influences the distribution of different species of fungi based on which litter or soil horizon they feed on (Ladygina, Caruso and Hedlund 2008).

The soil and litter profiles are categorized by the different gradients of microclimate and microhabitats. Early soil studies argued that the soil fauna did not form well defined communities because it was difficult to find associations between the vegetation types and the other features of the habitats (Anderson 1977). However, more recent studies believe that it should be possible to relate the different communities to external factors in the habitats (Setälä, Marshall and Trofymow 1995). Collembolan communities are known for being vertically structured with different species occurring on the surface, in the litter and in different layers of the soil profile (Chahartaghi, Langel, Scheu and Ruess 2005, Jorgensen, Elmholt and Petersen 2003, Rusek 1998, Salamon, Scheu and Schaefer 2008). These specializations reflecting the range in resource utilization, ranging from fresh litter to humified substances may to some extent explain the high species diversity in the soil (Huhta and Hänninen 2001). However, as most species appear to be food generalist and thus potential competitors, the diversity is far from being understood. Often closely related species replace each other in different habitat-/micro-habitat types (Hertzberg, Leinaas and Ims 1994, Leinaas and Fjellberg 1985). It is still unknown to what degree species interaction is important in the structure of collembolan species assemblages and whether it influences the presence/absence of collembolan species in different habitats. A substantial degree of specialization can reduce the specific interactions and thereby make it easier for species to co-exist, while a large degree of resource competition could explain that closely related species become limited to different habitats. However, the limitation to different habitats could also be due to specialization so the species are present in different habitats regardless of the presence of the other, closely related species (Leinaas and Fjellberg 1985). These are questions of great importance to improve our understanding of the structure and functioning of the soil ecosystem, including decomposition processes and mineralization of nutrient elements.

Temperature is an important determinant of collembolan activity. Significant changes in temperature have been shown to influence metabolism, reproduction, and development in soil arthropods (Birkemoe and Leinaas 2000, Birkemoe and Leinaas 2001, Uvarov 2003). Direct effects of temperature changes include increase in metabolism and thus growth and development rates (Birkemoe and Leinaas 2000, Birkemoe and Leinaas 2001), while indirect effects may involve a series of responses, ranging from size and stage of maturation (Birkemoe and Leinaas 2000) to changes in food resources and habitats (Cassagne, Spiegelberger, Cécillon, Juvy and Brun 2008). Different species have different requirements to their habitat with regards to the conditions that are optimum for growth and reproduction, and these requirements may also be influenced by temperature, like a decrease in the overall development time which again increases population growth (Haimi, Laamanen, Penttinen, Räty, Koponen, Kellomäki and Niemelä 2005, Jensen, Leinaas and Hessen 2006). Moreover, adult individuals of a species will probably have different needs than juvenile individuals of the same species (Cassagne, Spiegelberger, Cécillon, Juvy and Brun 2008, Haimi, Laamanen, Penttinen, Räty, Koponen, Kellomäki and Niemelä 2005, Huhta and Hänninen 2001, Jensen, Leinaas and Hessen 2006, Uvarov 2003), and thus experimental studies on species intaaction should include all life stages.

Based on the background presented above, I have investigated the interactions between two closely related collembolan species, *Folsomia quadrioculata* and *Folsomia manolachei* in microcosms with natural soil, and how the two species are affected by different types of soil and temperature. The duration of the experiments were chosen in order to get more than one generation of the species (Nygard and Solberg 1985). *F. quadrioculata* is widely distributed throughout the Holarctic, from the warm part of the temperate zone to the high Arctic (Fjellberg 1980, Gisin 1960, Hertzberg, Leinaas and Ims 1994), while *F. manolachei* has a more restricted distribution both in geographic range and habitats (Fjellberg 1980, Potapow 2001). In the Oslo area in Norway the two species differs in occurrence in forest habitats (H.P.Leinaas unpublished observations). *F. quadrioculata* is often numerous in raw humus from richer types of coniferous forests on podzol, *F. manolachei* does not appear to be present in these habitats. However, the latter species is common in mold from grey-brown podzolic soil where also *F. quadrioculata* may occur in low number and much less numerous than *F. manolachei*.

The purpose of the experiments was to investigate if the interaction between the two species could explain the different patterns of distribution of these two soil types. More specifically, I wanted to compare the growth of the populations of the species when they were kept alone and together in microcosms containing natural soil of the two different types. In doing so, I wanted to test the following hypotheses:

I. In one-species microcosms each species will do best in the type of soil where it is most numerous in nature.
II. For each soil type the species that is most numerous in that soil type in nature, will do best in the one-species microcosms.
III. In the two-species microcosms, the presence of one species will have a negative effect on the population growth of the other species, compared to how the species does in the one-species microcosms, and this effect will be greatest for the species that is absent or have the lowest density in the particular soil type in nature.
IV. Temperature (10^{o}-20^{o}) will not have an effect on the outcomes of the tests mentioned above.

As a basis for this study, I also measured the individual growth of both species in the two soil types and at the two testing temperatures.

MATERIAL AND METHODS

I. The species

The Collembola used in this experiment were lab-grown *Folsomia quadrioculata* and *Folsomia manolachei* from Denmark. I did not have access to lab-grown *F. manolachei* from Norway, only *F. quadrioculata*, so I decided to use both *F. quadrioculata* and *F. manolachei* from Denmark in order to make sure the species were adapted to the same climate. Both *F. quadrioculata* and *F. manolachei* had been kept in lab-cultures for 2-3 years at 15^{o}C, which accounts for more than 10 generations.

F. quadrioculata is a widely distributed Holarctic species and its presence has also been recorded all over Europe and Northern Asia. *F. quadrioculata* was interpreted to be a very common species around the world in early publications, but during the last decades it has become clear that the former *F. quadrioculata* s.l. in fact was a complex of several species. In Europe this also included *F. manolachei* (Potapow 2001, Wetton 1987) . So even though *F. quadrioculata* still is one of the most widespread collembolan species in the Palaearctic, the ecological preferences for the species have been redefined. *F. quadrioculata* can occur in the same areas as *F. manolachei*, but *F. quadrioculata* is usually found in more humid habitats and extends its distribution into colder areas than *F. manolachei* (Potapow 2001). *F. quadrioculata* is for instance common all over the high Arctic (Hertzberg, Leinaas and Ims 1994, Potapow 2001).

F. manolachei also has a wide distribution and it has been recorded in almost all the European countries and probably has a wide distribution in Asia as well, although most likely not as common in Asia as in Europe. *F. manolachei* can occur together with *F. quadrioculata* but usually prefers habitats that are dryer and warmer than the areas where *F. quadrioculata* is found. It has for instance not been recorded in the Arctic (Potapow 2001).

F. quadrioculata usually has a body length of up to 1.3 mm, and the color of the animals ranges from pale grey to almost black, while *F. manolachei* is a little smaller with a body length of up to about 1.0-1.2 mm, and usually has a darker colored body than *F. quadrioculata* (Fjellberg 1980, Potapow 2001).

II. Type of soil used

Grey-brown podzolic soil is the typical soil found in deciduous forests and woodland. The humus here is thoroughly mixed with the mineral soil and is named mold. For this study, mold was collected in a stand of deciduous trees outside the University of Oslo, Blindern, Norway. Podzol soil is typical for coniferous forests where the humus is typically accumulated above the mineral soil and is interwoven with mychorriza. This type of humus is called raw humus. For this study, the raw humus was collected from a coniferous forest at Nordmoen, about 80 km north of Oslo.

III. Experimental study

This experiment consisted of two parts. The main part tested the effect of soil type and temperature (10 vs. 20^{o}C) on population growth and species interaction. In an additional part I also investigated the effect of the same parameters on body growth rates. The population growth and species interaction experiment was conducted to find out which of the two species would do best in each soil type and at each temperature, and if there was a difference in the outcomes when the species were in separate one-species microcosms or together in species-interaction microcosms. The study on the body growth rates was conducted to find out if there is a difference in the rate of body growth for *F. quadrioculata* and *F. manolachei* with regards to different soils and temperatures, as it was believed that such information might contribute to the understanding of the outcome of the population growth experiments.

The population growth and species interaction experiment was conducted using adult laboratory reared individuals of both species. The experimental boxes (microcosms) were 3 cm long with a 3.5 cm diameter and filled with the chosen soil type. Each box had 5 wholes, 1 cm in diameter, 1 on the bottom, 1 on the top, and 3 evenly distributed around the sides, that were covered with 50µm meshes to make sure moisture could enter the experimental boxes but prevented the Collembola from escaping. The soil used in this experiment was defaunated by freezing it down to -70-80^{o}C and then keep them at room temperature for 2 days before Collembola were placed in the microcosms.

Intact raw humus profiles were transferred directly from the soil to the microcosms in the field by means of a corer with the same diameter as the experimental box. All the vegetation was removed, except for the lowest ca. 5 mm of green mass, and the soil corer was cut at a depth of ca. 2.5 cm below the green moss, before it was placed in the boxes (Figure 1).

Figure 1A: Intact raw humus profile in an experimental box

Figure 1B: Intact mold profile in an experimental box

The mold was too loose and full of large objects such as roots and stones to be sampled intact by the corer. Instead the upper 2.5-3 cm of the soil was removed using a spade and brought to the lab. There, the large objects were sorted out by a 2 mm sieve and the microcosms boxes filled with 2.5 cm soil. At the sampling site the ground was almost bare, with no moss or other vegetation, and litter present. Thus the microcosms consisted of mold soil only.

The experiment was conducted in two climate rooms (floor: 2.1m x 1.9 m; height: 3.2 m) at 10^{o}C and 20^{o}C. I carried out experiments with both mold and raw humus in each room. The boxes were kept on a table 75 cm above the floor and with a light regime of L:D = 16:8 (Figure 2).

At each temperature I started with 20 individuals of each species in 15 one-species experimental boxes with mold, for both *F. quadrioculata* and *F. manolachei,* and 15 one-species experimental boxes with raw humus, for both *F. quadrioculata* and *F. manolachei*, so there were 120 one-species boxes in all. And in addition, 40 individuals (20 of each species) in 15 interaction experimental boxes with mold and 15 interaction experimental boxes with raw humus, so there were 60 interaction boxes in all. The interaction boxes (*F. quadrioculata* + *F. manolachei*) had 20 individuals of each species because my null hypothesis is that there is no competitive interaction between the two species. Consequently, the presence of one species should not affect the other species in the microcosms, and therefore, the initial population of 20 individuals of one species should show the same growth independently of the presence of the other species.

In order to avoid systematic effects du to any possible gradient (temperature, light etc) within the climate rooms, the microcosms boxes were placed randomly in 4 larger containers, 22 x 17 cm, filled with vermiculite. 2 containers were used at each temperature. The experimental boxes with mold were randomly placed in one of the large plastic boxes, while the experimental boxes with raw humus were randomly placed in the other large plastic box. The microcosms boxes were dug into the vermiculite, so the top of the boxes were in line with the surface of the vermiculite. The plastic boxes were placed on a table, 75 cm above the floor (Figure 2). After the experiment started the vermiculite was checked regularly and distilled water was added to keep the environment moist for the Collembola. In order to prevent too strong water evaporation from the containers, they were covered by plastic foil that was kept ca. 1 - 1.5 cm above the top of the containers to allow aeration.

Figure 2: Micro-cosmos in a large plastic box with vermiculite placed in a climate chamber

The microcosms were kept at 10^{o}C for six months and at 20^{o}C for three months. This difference in duration was based on the result of Nygard and Solberg (1985).

After the population growth and species interaction experiment ended the Collembola were driven out of the soil by a MacFadyen High Gradient extractor (Macfadyen 1961), in order to fin out how the Collembola did in different soils and at different temperatures (Figure 3). Plastic boxes, length 3 cm and diameter 3.5 cm, where filled up with ~1 cm 50% benzoic acid. The top of these boxes was covered with a net with 1 mm quadratic wholes that was kept in place by a red plastic ring. A brown cylinder, with the same length and diameter as the experimental boxes, was placed top of the net, inside the red plastic ring. The soil from the experimental boxes was transferred upside down into the brown cylinders, where the net kept the soil from falling into the benzoic acid (Figure 4). After the soil from all the experimental boxes were transferred to the brown cylinders on the top of the boxes with 50% benzoic acid, the entire setup with the experimental boxes containing the net, red plastic ring, and brown cylinder, were transferred to the MacFadyen High Gradient extractor. The experimental boxes were separated from each other by Styrofoam (Figure 3). The soil extraction process took five days. By means of a cooling below and gradual increasing temperature above, an increasing temperature gradient was created across the soil samples. This temperature gradient and the resulting drying of the soil samples move the Collembola through the soil core until they fall into and are killed by the benzoic acid. After five days the soil samples were completely dried out, and the animals efficiently extracted out (Leinaas 1978b, Macfadyen 1961). The Collembola were subsequently transferred from the box with 50% benzoic acid to a similar box containing 70% alcohol, in order to preserve the Collembola.

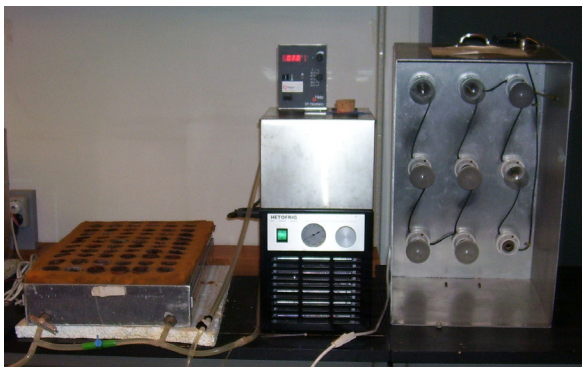

Figure 3: The MacFadyen High Gradient with the separating Styrofoam on the bottom

Figure 4: Set-up of experimental boxes before they put into the MacFadyen extractor

After the experiment was finished the Collembola from each experimental box were counted. In the interaction boxes the two species were sorted, based on the abdomen terminal macroseta length (Wetton 1987), before counted. The results of the sorting and counting showed how well *F. quadrioculata* and *F. manolachei* had done in the different soils (mold and raw humus) and at different temperatures, and also if there was a difference when the species were alone in the experimental boxes compared to when they were together in an interaction box.

The body growth rate part of the experiment was designed to compare the effect on growth rate in two soil types (mold and raw humus) at two temperatures (10°C and 20°C) and started with eggs that were collected from lab-grown *F. quadrioculata* and *F. manolachei*. As a standard, all individuals came from eggs that had developed at 15°C. The eggs were kept in plastic boxes, height 3 cm and diameter 3.5 cm, with clean plaster of Paris and charcoal mixture covering the bottom of the boxes (Rohde 1956). The eggs were inspected daily, and the newly hatched Collembola were transferred to experimental boxes, similar to those that the eggs had been kept in. However, in the experimental boxes the bottom above the plaster of Paris and charcoal mixture, was supplied with a thin cover (~2 mm) with sieved (1 mm mesh) soil (mold or raw humus) as food substrate for the animals. Before sieving, the soil had been frozen down to -20°C twice, with a one day interval at room temperature between the freezing sessions, in order to kill arthropods present in the soil but not destroy the microflora.

The body growth experiment was conducted in the same climate rooms as described above. I used mold or raw humus soil in separate boxes at each temperature. The boxes were kept on a table 75 cm above the floor and with the same light regimes as described above. Each box started with approximately 2 mm of soil on top of the plaster of Paris and charcoal bottom. I had 9 boxes with each species (*F. quadrioculata* and *F. manolachei*) in both soils (mold and raw humus) at both temperatures (10°C and 20°C), totaling 36 experimental boxes at each temperature, 72 experimental boxes in all. The growth was measured after 2, 4, and 8 weeks in all the treatments.

Half of the soil in the boxes was removed and replaced with fresh soil every two weeks during the experiment to make sure the Collembola had enough food. During this replacement a few drops of distilled water were added to the plaster of Paris and charcoal bottom to make sure the boxes were moist and did not dry out. During the soil replacement half of the soil was removed by taking out small pieces one by one and checking them under the microscope to make sure no collembolans were in the soil being removed, and the top of the experimental boxes was put back on after each removal to make sure none of the collembolans escaped during the soil replacement.

When the Collembola were sampled, after 2, 4, and 8 weeks, they were put in 70% alcohol for preservation. The growth of the Collembola was measured by analyzing pictures taken with a 6x magnification by using a camera, Nikon D300, which was attached to a microscope. The pictures were analyzed using the Image J program. Each Collembola was measured using the program and data was then imported into excel where the measurements were converted from pixels to millimeter in order to compare the growth.

RESULTS

I. Population growth and species interaction

This experiment is looking at the interaction between *F. quadrioculata* and *F. manolachei* in mold and raw humus soil at 10°C and 20°C. *F. quadrioculata* did better than *F. manolachei* both in one-species boxes and in interaction boxes at 10°C in mold (Figures 5 and 6). *F. quadrioculata* survived in many more boxes than *F. manolachei*, and in the surviving populations the numbers of animals were high for *F. quadrioculata* in both situations. This was most clearly seen in the single-species boxes of each of the two species. One exception was the dramatically strong growth in one single population of *F. manolachei*. The results clearly show that *F. quadrioculata* had a dramatically higher success in single species boxes compared to interaction boxes both in terms of number of individuals and population survival in mold. *F. manolachei* show the same tendency of doing better alone than in the interaction boxes, however for this species the result was to some extent obscured by the high extinction rate in both treatments. The statistical tests that were performed did not find any significant effects with regards to the interaction between the two species and could not give a good indication for the differences that are seen between the two species in mold at 10°C (Table 1).

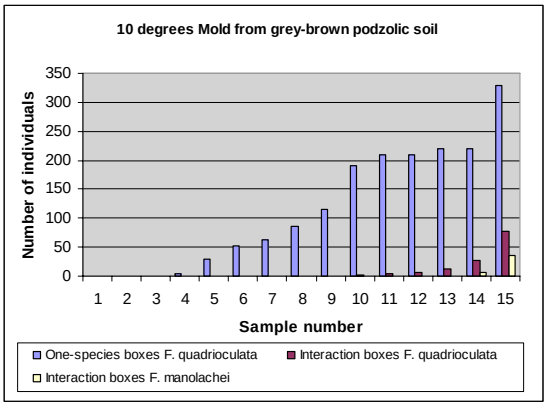

Figure 5: Number of *F. quadrioculata* individuals that survived in one-species boxes in mold at 10°C, in the order of fewest to highest number of individuals in the sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

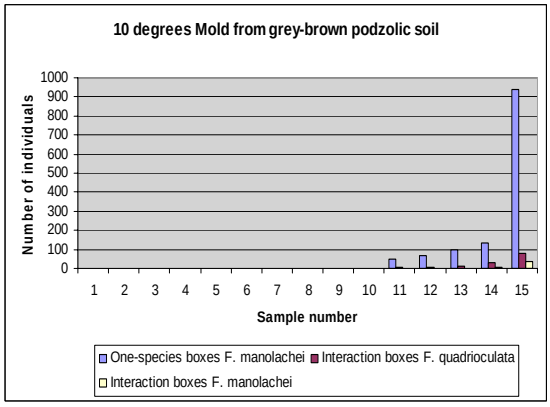

Figure 6: Number of *F. manolachei* individuals that survived in one-species boxes in mold at 10°C, in the order of fewest to highest number of individuals in that sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

For both species the final population sizes in mold soil were much smaller at 20°C than at 10°C. In fact, all populations showed a decline in number of individuals by the end of the experiment (Figures 7 and 8). However, at this temperature *F. manolachei* appeared to have done better than *F. quadrioculata* in the one-species boxes, while *F. quadrioculata* did better than *F. manolachei* in the interaction boxes (Figures 7 and 8). The statistical analyses show that there is a significant effect of temperature for both *F. quadrioculata*, with a 24% reduction in numbers from 20°C to 10°C, and a 23% reduction in numbers for *F. manolachei* from 20°C to 10°C (Table 1). More surprisingly, *F. quadrioculata* did better in interaction boxes than in one-species boxes (Figure 7), while *F. manolachei* did better in separate boxes than in interaction boxes in this treatment (Figure 8). This surprising result cannot be explained by the statistical analyses performed because they did not show any significant effects for the interaction between the two species.

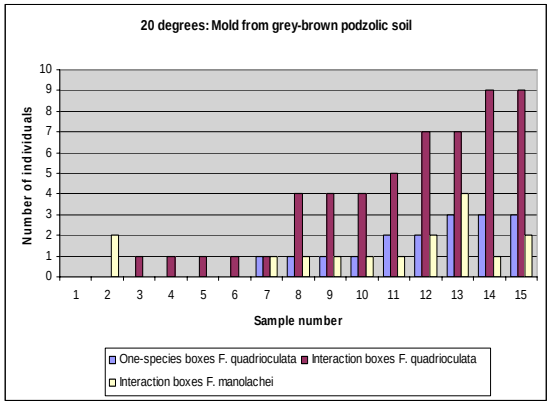

Figure 7: Number of *F. quadrioculata* individuals that survived in one-species boxes in mold at 20°C, in the order of fewest to highest number of individuals in the sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

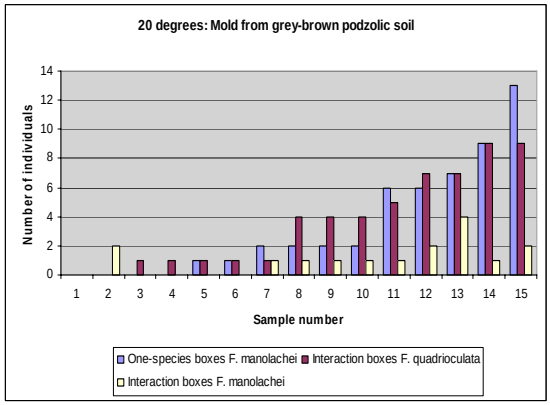

Figure 8: Number of *F. manolachei* individuals that survived in one-species boxes in mold at 20°C, in the order of fewest to highest number of individuals in that sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

According to the first hypothesis for this experiment, *F. manolachei* should do better in one-species boxes in mold than *F. quadrioculata*, but this is not the case, *F. quadrioculata* has done much better than *F. manolachei* in one-species boxes in mold, at both temperatures. However, *F. manolachei* did better in one-species boxes than in interaction boxes with mold as I predicted in my second hypothesis, the presence of *F. manolachei* in interaction boxes is having a negative effect on the population growth for *F. quadrioculata* in mold, and the outcomes of these tests are not influenced by temperature, which is my third and fourth hypotheses.

The results from the microcosms with raw humus placed at 10°C are shown in Figures 9 and 10. *F. quadrioculata* appear to have done better than *F. manolachei* in both one-species boxes and in interaction boxes with this treatment. Unlike what is seen in the mold treatment, both species survived in all microcosms with raw humus throughout the experiment. *F. quadrioculata* did slightly better in one-species boxes than in combination boxes with *F. manolachei* (Figure 9). One of the interesting things here is that the 3 samples of interaction boxes with the lowest number of *F. quadrioculata* also have the lowest number of *F. manolachei* (Figures 9 and 10).

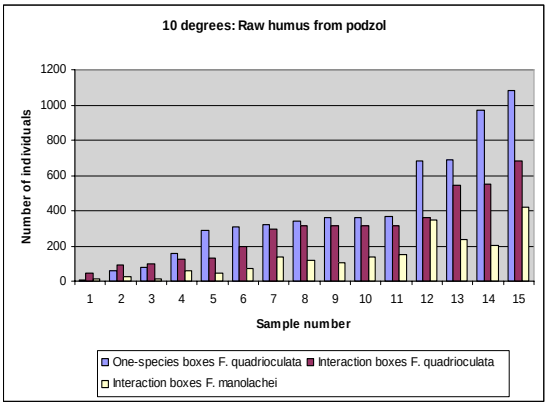

Figure 10: Number of *F. quadrioculata* individuals that survived in one-species boxes in raw humus at 10°C, in the order of fewest to highest number of individuals in the sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

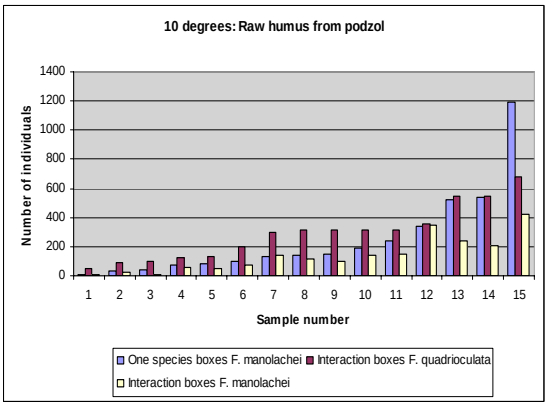

Figure 11: Number of *F. manolachei* individuals that survived in one-species boxes in raw humus at 10°C, in the order of fewest to highest number of individuals in that sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

F. quadrioculata did much better in one-species boxes and interaction boxes with raw humus at 20°C than *F. manolachei* (Figures 12 and 13). Except for two samples of *F. manolachei* in one-species boxes, the species survived in all the other experimental boxes with this treatment. *F. quadrioculata* had a higher success in one-species boxes compared to interaction boxes, while *F. manolachei* does slightly better in interaction boxes than in one-species boxes in raw humus at 20°C.

The results from raw humus are similar to the results from mold in that the final population sizes were much smaller at 20°C than at 10°C. This coincides with the statistical results that show a significant effect of temperature. The statistical analyses also showed that there is a significant effect of soil with *F. quadrioculata* having a 41% increase in numbers from mold to raw humus, and *F. manolachei* having a 32% increase in number from mold to raw humus, and this is also apparent by looking at Figures 1 through 10, which shows a significant increase of individuals for both species in raw humus compared to mold, at both temperatures.

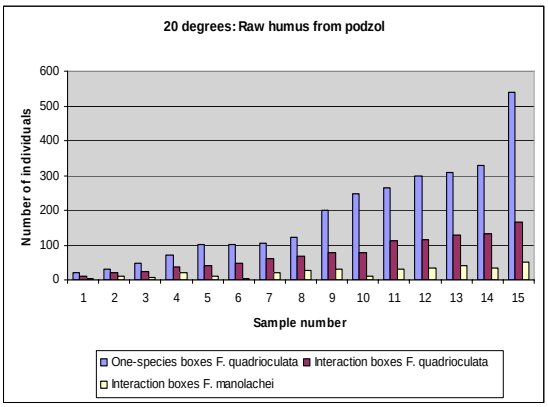

Figure 12: Number of *F. quadrioculata* individuals that survived in one-species boxes in raw humus at 20°C, in the order of fewest to highest number of individuals in the sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

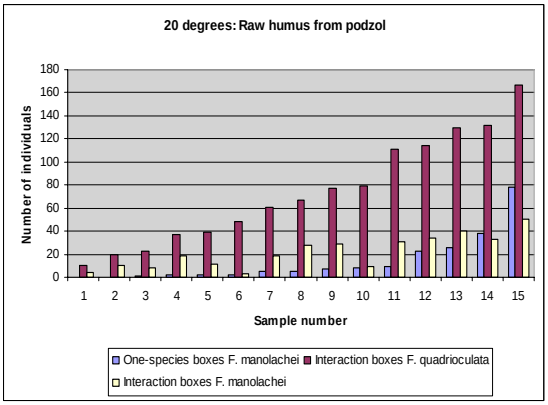

Figure 13: Number of *F. manolachei* individuals that survived in one-species boxes in raw humus at 20°C, in the order of fewest to highest number of individuals in that sample. Together with the number of *F. quadrioculata* and *F. manolachei* that survived in the interaction boxes. The sample numbers for the interaction boxes show the number of *F. quadrioculata* and *F. manolachei* that survived together in the actual experimental boxes.

The results from the experimental boxes with raw humus were as expected with *F. quadrioculata* doing very well and *F. manolachei* having a negative effect on *F. quadrioculata* in interaction boxes. Temperature did not have an effect on these results, so all my hypotheses are supported with the results from raw humus.

Response variable	Predictor variable	Estimate	Std. Error	Pr(>|z)
F. manolachei	Temperature 20C	- 1.4504	0.4833	0.00269
	Soil: Raw humus	3.4766	0.3604	<2e-16
	Interaction	- 0.4514	0.4833	0.35034
F. quadrioculata	Temperature 20C	- 1.4192	0.4586	0.00197
	Soil: Raw humus	3.7169	0.2911	<2e-16
	Interaction	-0.7400	0.4586	0.10662

Table 1: Statistical analyses on population growth and species interaction based on the lmer function in R, version 2.8.1, due to over dispersion with the GLM-analysis. The results seen here are the outcomes of the changes seen from 10°C to 20°C and from mold to raw humus.

II. Body growth rates

The individual growth of both *F. quadrioculata* and *F. manolachei* were measured in the body growth rate part of the experiment as a basis for the population growth and species interaction.

The average growth of *F. quadrioculata* and *F. manolachei* in mold soil at 10°C from newly hatched until they are 8 weeks old are shown in Figure 14. *F. quadrioculata* is on average larger than *F. manolachei* when they are newly hatched and at every age interval after that. Similarly, average growth in mold soil at 20°C is illustrated in Figure 15. The results from 20°C appear very similar to those from 10°C, but at 20°C both species showed little growth between 4 and 8 weeks. The statistical analyses show that the effect of soil is significant for *F. manolachei* at 4 weeks, while there are significant effects of both temperature and soil for *F. quadrioculata* at 4 weeks (Table 2). The results from the statistical analyses also indicates that it is an significant effect of temperature for *F. manolachei* at 2 weeks, however, this particular result has over dispersion, so it is not a reliable observation.

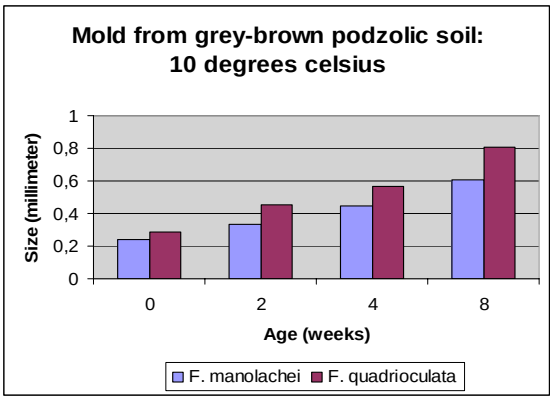

Figure 14: The average size, in millimeter, of *F. quadrioculata* and *F. manolachei* at hatching (week 0) and their subsequent average growth in mold at 10°C after 2, 4, and 8 weeks.

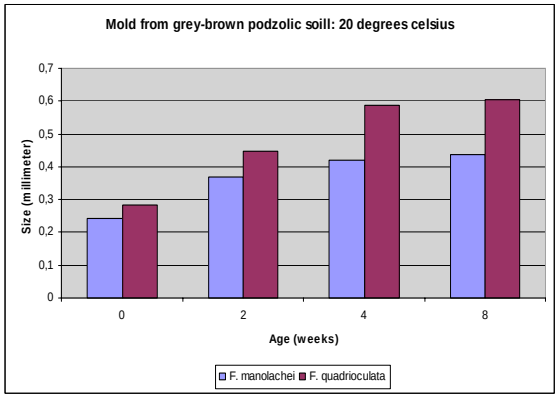

Figure 15: The average size, in millimeter, of *F. quadrioculata* and *F. manolachei* at hatching (week 0) and their subsequent average growth in mold at 20°C after 2, 4, and 8 weeks.

The growth of *F. quadrioculata* and *F. manolachei* in raw humus at 10°C is shown in Figure 16. The growth patterns appear fairly similar to what is seen in the mold soil. The difference between the species seems more pronounced in raw humus at 20°C (Figure 17) than at 10°C. Except for an unexplainable apparent arrest in growth between 2 and 4 weeks, the figure suggests that the difference in growth rate increases with time. By 8 weeks *F. quadrioculata* had become on average nearly twice as long as *F. manolachei.*

The statistical analyses for the body growth rate (Table 2) show that soil has a significant effect on the growth rate for *F. manolachei* at 4 weeks, and at 8 weeks both soil and temperature have significant effects on the growth rate for *F. manolachei*. Contrary to the results for *F. quadrioculata* which show significant effects of both soil and temperature at 4 weeks, and only soil has a significant effect on the growth rates at 8 weeks.

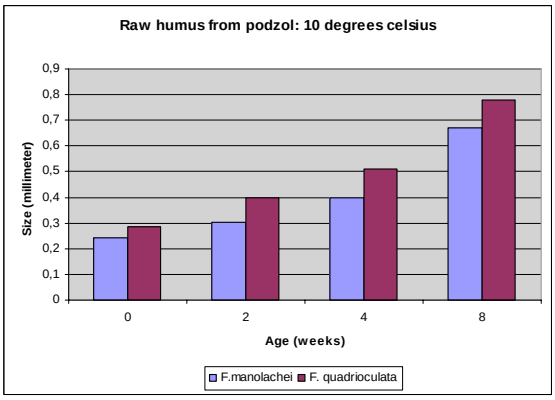

Figure 16: The average size, in millimeter, of *F. quadrioculata* and *F. manolachei* at hatching (week 0) and their subsequent average growth in raw humus at 10°C after 2, 4, and 8 weeks.

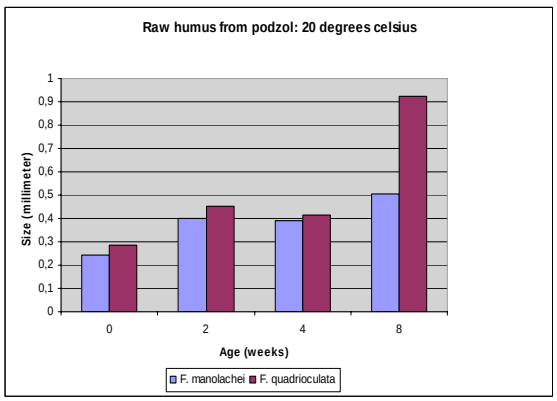

Figure 17: The average size, in millimeter, of *F. quadrioculata* and *F. manolachei* at hatching (week 0) and their subsequent average growth in raw humus at 20°C after 2, 4, and 8 weeks.

Response variable	Predictor variable	Estimate	Std. Error	Pr(>|z|)
F. manolachei: 2 weeks	Temperature 20C	0.068424	0.009328	<2e-16
	Soil: Raw humus	0.001594	0.011521	0.89
F. manolachei: 4 weeks	Temperature 20C	- 0.02097	0.02029	0.304
	Soil: Raw humus	- 0.04217	0.02022	0.0399
F. manolachei: 8 weeks	Temperature 20C	- 0.17857	0.02396	7.45e-11
	Soil: Raw humus	0.09483	0.2938	0.00178
F. quadrioculata: 2 weeks	Temperature 20C	0.024612	0.012867	0.0587
	Soil: Raw humus	-0.020046	0.012922	0.124
F. quadrioculata: 4 weeks	Temperature 20C	-0.05402	0.02492	0.0329
	Soil: Raw humus	-0.14051	0.02008	5.39e-10
F. quadrioculata: 8 weeks	Temperature 20C	-0.02194	0.03510	0.533
	Soil: Raw humus	0.13903	0.03258	4.17e-05

Table 2: Statistical analyses on body growth rates based on the GLM-function in R, version 2.8.1. The results seen here are the outcomes of the changes occurring from 10^{o}C to 20^{o}C and from mold to raw humus.

DISCUSSION

The first hypothesis I addressed was that in the one-species microcosms the species will do best in the type of soil where it is most common. This was true for *F. quadrioculata* who did best in raw humus; however, there are some unexpected findings for the boxes with mold at 20^{o}C. *F. manolachei* does better in one-species boxes than *F. quadrioculata*, which is expected, however, *F. quadrioculata* that are in interaction boxes with *F. manolachei* have a higher number of individuals than *F. quadrioculata* in one-species boxes. This is difficult to explain since the statistical analyses performed during this experiment did not show any significant effects of the interactions between the two species, and based on other studies, *F. quadrioculata* is normally absent from these areas in natural settings, so *F. manolachei* should do better than *F. quadrioculata* in this soil type. One microcosm with *F. manolachei* did very well in mold at 10^{o}C, but this was the exception.

The fact that the mold soil was sieved before it was added to the experimental boxes could be a contributing factor for the experimental boxes with mold not having optimal living conditions for the species. So it is possible that *F. quadrioculata* managed to survive and do better than *F. manolachei* in a habitat that did not have optimal conditions because they have different life history traits than *F. manolachei*.

The results from the experimental boxes with raw humus, at both temperatures, were as expected, with *F. quadrioculata* doing very well and *F. manolachei* having a negative effect on *F. quadrioculata* in interaction boxes. Even though the statistical analysis in this experiment does not show a significant effect of interaction between the two species, it does appear on the diagrams that *F. manolachei* contributes to a negative effect of population growth for *F. quadrioculata* when they are in interaction boxes. One explanation for the unexpected results in this study is that there are several factors influencing the population growth of the two species, and this study is only looking at two aspects of the soil web.

Based on the findings by Nygard and Solberg (Nygard and Solberg 1985), I expected that higher temperatures would result in faster development, so both *F. quadrioculata* and *F. manolachei* should on average be larger in 20^{o}C mold compared to 10^{o}C mold and in 20^{o}C raw humus compared to 10^{o}C raw humus. This was only the case for *F. quadrioculata* in raw humus at 20^{o}C. *F. manolachei* was on average larger in 10^{o}C mold and 10^{o}C raw humus, than in 20^{o}C mold and 20^{o}C raw humus, while *F. quadrioculata* was on average larger in 10^{o}C mold than in 20^{o}C mold. This could again be an indication that the growth conditions in the experimental boxes were not optimal; it could for instance be possible that the species did not have enough nutrients in the boxes or the humidity was not optimal.

The body growth rate experiment showed that on average *F. quadrioculata* obtained the largest size of the species after 8 weeks in raw humus at 20^{o}C. On average *F. manolachei* only got to about half the size of *F. quadrioculata* in the same treatment which can be partially explained by the statistical analyses showing significant effects of soil for both species after 8 weeks. Both *F. quadrioculata* and *F. manolachei* had little growth between 2 and 4 weeks, the average size of *F. quadrioculata* is actually a little lower after 2 weeks compared to 4 weeks. Again the statistical analyses show significance of soil for both species after 4 weeks and in addition significance of temperature after 4 weeks for *F. quadrioculata*. This is probably an indication that the experimental boxes did not have optimal growth conditions for *F. quadrioculata* and *F. manolachei*.

In field studies conducted by Hairston (1980) on terrestrial salamanders that had a broad or narrow habitat overlapping, Hairston found that species with narrow habitat overlapping had a relatively strong competition between them, while the species with a broad habitat overlap did not have much competition. This kind of pattern can be explained by species with similar habitat requirements competing for the same habitat, the competition can be so tough in some areas forcing the species to get excluded from part of their potential habitat (Hairston 1980). Although I have shown competition could be a factor explaining why *F. quadrioculata* do not occur in high densities in mold and *F. manolachei* do not occur naturally in raw humus, other factors and habitat specifics are probably influential as well, since this experiment has shown that *F. quadrioculata* is quiet capable of living and reproducing in mold and *F. manolachei* can also live and reproduce in raw humus.

One of the interesting things with this experiment is that I have shown that *F. manolachei* has the ability to live and reproduce in raw humus, even though they are not usually found naturally in this habitat and *F. quadrioculata* have the ability to live and reproduce as well as, or better than *F. manolachei* in mold soil, both when they are in one-species boxes and when they are in interaction boxes. This implies that there are other factors, in addition to competition and type of soil, which influences where *F. quadrioculata* and *F. manolachei* live and thrive in natural conditions.

The humus form is a result of the interactions in the soil food web between primary producers and decomposers, and these interactions are influenced by environmental factors like temperature (Cassagne, Spiegelberger, Cécillon, Juvy and Brun 2008). The different types of humus forms have different soil features like soil pH, moisture and availability of nutrients and this must be taken into account when we try to understand the relationships between the soil invertebrates and the plants (Jørgensen, Hedlund and Axelsen 2008). Several studies have looked at how individual Collembola species responds to the different habitat factors, like the amount of organic matter, however, most of these studies have not considered how the Collembolan community is influenced by these factors (Hasegawa 2002). A study conducted by Abbott and Crossley found that the amount of soil organic matter and the organization of this organic matter influences the organization of the Collembola community in the soil (Abbott and Crossley 1982). Another study by Cole and associates also found that the abundance of Collembola, and other microarthropods, increased with increased soil fertility, however, the diversity of Collembola, and other microarthropods, did not change with the increased soil fertility (Cole, Buckland and Bardgett 2005). This is supported by the findings in this study that the type of soil had significant effects for the outcome of *F. quadrioculata* and *F. manolachei* in the different soils.

Soil warming experiments that have been conducted in boreal and arctic ecosystems (Cassagne, Spiegelberger, Cécillon, Juvy and Brun 2008, Dollery, Hodkinson and Jonsdottir 2006, Haimi, Laamanen, Penttinen, Räty, Koponen, Kellomäki and Niemelä 2005, Lindberg, Engtsson and Persson 2002, McGeoch, Le Roux, Hugo and Chown 2006, Sjursen, Michelsen and Jonasson 2005) have found that the density of Collembola decreases with increased temperature. This is also something we can apply to mold and raw humus habitats based on the results from this study, both *F. quadrioculata* and *F. manolachei* had a reduction in number of individuals that survived, in both soils, with increased temperature.

The interaction that we see between species and patchy habitats depends on the species ability to utilize the habitat based on the species life history and their mobility and the habitats ability to influence the development of the species (Hertzberg, Yoccoz, Ims and Leinaas 2000). Patchiness of a habitat can be defined in different ways: a habitat can have a patchy distribution of resources or a patchy distribution of the habitat itself, and both these aspects have the ability to split different populations into subpopulations (Hertzberg, Leinaas and Ims 1994). The different species of Collembola have develop characteristic life history traits based on selective pressures in the different habitats in order to maximize their fitness for the ecological niche they live in (Hopkin 1997). Even though there were some problems with the mold treatment in this experiment, the results give support to specialization in order to maximize fitness. So even though both species can survive and reproduce in each others habitat, in the long run it is probably more productive for *F. quadrioculata* to stay in raw humus instead of broaden their habitats into mold, and vice versa for *F. manolachei*.

CONCLUSION

The results from the experimental boxes with raw humus, at both temperatures, were as expected, with *F. quadrioculata* doing very well and *F. manolachei* having a negative effect on *F. quadrioculata* in interaction boxes.

Faster development due to higher temperatures were observed for *F. quadrioculata* in raw humus at 20^{o}C, however, *F. manolachei* was on average larger in 10^{o}C mold and 10^{o}C raw humus, than in 20^{o}C mold and 20^{o}C raw humus, while *F. quadrioculata* was on average larger in 10^{o}C mold than in 20^{o}C mold which is not what I expected. However, this study supports findings of other studies in that the type of soil had significant effect for the outcome of *F. quadrioculata* and *F. manolachei* in the different soils. In addition both *F. quadrioculata* and *F. manolachei* show a reduction in number of individuals that survive, in both soils, with increased temperatures wich supports the findings of other soil warming experiments, which show that the density of Collembola decreases with increased temperature.

An exciting outcome of this experiment is that I have shown that *F. manolachei* has the ability to live and reproduce in raw humus, even though they are not usually found naturally in this habitat and *F. quadrioculata* have the ability to live and reproduce as well as, or better than *F. manolachei* in mold soil, both when they are in one-species boxes and when they are in interaction boxes. This implies that there are other factors, in addition to competition and type of soil, which influences where *F. quadrioculata* and *F. manolachei* live and thrive in natural conditions.

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