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Soil microbes weaken the positive effect of an aquatic–terrestrial subsidy on plant performance

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Abstract

Aims Linkages formed through aquatic–terrestrial subsidies can play an important role in structuring communities and mediating ecosystem functions. Aquatic–terrestrial subsidies may be especially important in nutrient-poor ecosystems, such as the freshwater sand dunes surrounding Lake Michigan. Adult midges emerge from Lake Michigan in the spring, swarm to mate and die. Their carcasses form mounds at the base of plants, where they may increase plant productivity through their nutrient inputs. However, the effect of aquatic–terrestrial subsidies on plant productivity could depend on other biotic interactions. In particular, soil microbes might play a key role in facilitating the conversion of nutrients to plant-available forms or competing for the nutrients with plants.

Methods In a greenhouse experiment, we tested how carcasses from lake emergent midges (Chironomidae) and soil microbes independently and interactively influenced the performance of a common dune grass, *Calamovilfa longifolia*. To determine whether midges influenced abiotic soil properties, we measured how midge additions influenced soil nutrients and soil moisture.

Important Findings Midges greatly increased plant biomass, while soil microbes influenced the magnitude of this effect. In the absence of soil microbes plant biomass was seven times greater with midges than without midges. However, in the presence of soil microbes, plant biomass was only three times greater. The effect of midges might be driven by their nutrient inputs into the soil, as midges contained 100 times more N, 10 times more P and 150 times more K than dune soils did. Our results suggest that soil microbes may be competing with plants for these nutrients. In sum, we found that midges can be an important aquatic–terrestrial subsidy that produces strong, positive effects on plant productivity along the shorelines of Lake Michigan, but that the impact of aquatic–terrestrial subsidies must be considered within the context of the complex interactions that take place within ecological communities.

Keywords aquatic–terrestrial subsidies, *Calamovilfa longifolia*, lake emergent midges, sand dunes, soil microbes

土壤微生物削弱了水生-陆地系统补贴对植物生长的正向影响

摘要：水生-陆地系统补贴形成的联结作用在构建群落和调节生态系统功能方面发挥重要作用。在营养贫瘠的生态系统中(例如密歇根湖周围的淡水沙丘)，水生-陆生系统补贴显得尤为重要。春季成年蠓在密歇根湖涌出，成群交配，然后死亡。蠓尸体在植物的基部形成土丘状，通过输入营养提高植物的生产力。然而，水生-陆地系统补贴对植物生产力的影响可能取决于其他生物的交互作用，特别是土壤微

生物可能通过促进养分转化为植物可利用的形式或与植物竞争养分而发挥关键作用。在温室实验中，我们检验了湖生蠓(Chironomidae)的尸体和土壤微生物如何独立和相互影响一种常见沙丘草(沙拂子茅，*Calamovilfa longifolia*)的生长表现。为确定蠓是否影响土壤非生物特性，我们检验了添加蠓如何影响土壤养分和土壤湿度。研究结果显示，蠓极大地增加了植物生物量，但其效应的大小受土壤微生物的影响。在没有土壤微生物的情况下，添加蠓的植物生物量比没有添加的高7倍，而在有土壤微生物的情况下，植物生物量提高了3倍。蠓对植物生长的促进作用可能由于它们向土壤中输入养分所导致，因为与沙丘土壤相比，蠓的氮、磷、钾含量分别高100倍、10倍和150倍。我们的研究结果表明，土壤微生物可能与植物竞争这些养分。总之，我们发现蠓是重要的水生-陆地系统补贴，对密歇根湖沿岸植物生产力产生强烈和正向的影响，但水生-陆地系统补贴作用必须在生态群落内发生的复杂相互作用的背景下考虑。

关键词：水生-陆地系统补贴，沙拂子茅，湖生蠓，沙丘，土壤微生物

INTRODUCTION

Aquatic–terrestrial subsidies are flows of energy and nutrients derived from aquatic ecosystems to terrestrial habitats, and they can play an important role in structuring ecosystems and mediating ecosystem functions (Polis *et al.* 1997; Schindler and Smits 2017; Spiller *et al.* 2010). For example, the spawning migrations of salmon deposit fish carcasses near the shores of rivers and streams, and many terrestrial consumers are dependent on this aquatic subsidy (Gende *et al.* 2002). Terrestrial plants, too, benefit from the nitrogen deposited by salmon carcasses (Helfield and Naiman 2001). While much smaller in size, insects that spend part of their life cycle in aquatic ecosystems can also significantly influence terrestrial ecosystems. Midges that emerge as adults from Icelandic lakes provide resources for detritivores and predators (Gratton *et al.* 2008) and can alter terrestrial arthropod abundance (Dreyer *et al.* 2012; Hoekman *et al.* 2011) and community composition (Hoekman *et al.* 2019). The deposition of midge carcasses can also increase aboveground plant biomass and shift plant community composition (Gratton *et al.* 2017).

While little studied, the seasonal mass emergence of midges along the shores of Lake Michigan may represent an important aquatic–terrestrial subsidy. Midges (Chironomidae) spend their larval stage in freshwater, where they are an important resource for fish (Kornis and Janssen 2011). As they mature into their adult, flying form, midges congregate along shorelines in breeding swarms. Adult forms live for 5–10 days, and often die *en masse* (Fig. 1). The eastern shore of Lake Michigan is largely composed of sand dune ecosystems. The sand dunes are primary successional ecosystems; new dunes are formed approximately every 32 years and are stabilized by dune vegetation (Cowles 1899; Lichter 1998; Olson 1958). Soil nutrients are very low in the youngest dunes, which are closest to the shore (Lichter 1998; Olson 1958). Therefore, deposition of midges may provide an important nutrient source for early successional plants (Lundberg and Moberg 2003). Midge emergence from a neighboring Great Lake, Lake Huron, is an important subsidy for migrating birds (Ewert *et al.* 2011; Smith *et al.* 1998, 2004, 2007). However, whether midges influence plant performance in this system is unknown.

Soil microbes may play a critical role in mediating plant responses to midge deposition. During decomposition, microbes can quickly mineralize the nutrients in insect cadavers (Fielding *et al.* 2013), increasing the availability of nutrients to plants. Furthermore, root-symbiotic arbuscular mycorrhizal (AM) fungi can help plants compete for nutrients, including nitrogen and phosphorus, in the soil (Hodge and Fitter 2010; Smith and Read 1998; Whiteside *et al.* 2012). Increased nutrient availability from invertebrate cadavers can increase plant growth and plant quality (Bultman *et al.* 2014; Kos *et al.* 2017). In contrast, soil microbes may compete with plants for the nutrients contained in midges (Kuzyakov and Xu 2013), decreasing the positive effect of midge carcasses on plant performance. Competition for the nutrients in aquatic–terrestrial subsidies may be especially apparent in ecosystems with low soil organic material, like early successional sand dunes.

Using a greenhouse experiment, we tested how lake emergent midges and soil microbes influenced the performance of a common dune grass, *Calamovilfa*

Figure 1: Photograph of lake emergent midge carcasses trapped in vegetation along the shore of Lake Michigan at Sleeping Bear Dunes National Lakeshore.

longifolia. We hypothesized that midge carcasses will increase plant performance, but that the magnitude and/or direction of the effect may depend on the presence of soil microbes. To determine whether the effect of midges may be caused by changes in abiotic soil properties, we analyzed how midge additions influenced soil nutrients and soil moisture.

MATERIALS AND METHODS

Soil and midge collection

On 10 May 2019, we collected soil and midges from Sleeping Bear Dunes National Lakeshore, Empire, MI, USA. The midges were consistent with *Heterotrissocladius oliveri* (Diptera: Chironomidae), which is typically the most abundant chironomid species in Lake Michigan (Winnell and White 1986). Midges were swarming vegetation on dune ridges. We collected the midges with nets, stored them in plastic boxes and froze them. We collected approximately 75 g of midges (wet weight) in about 3 h. At the same location, soil was collected from underneath plants (primarily *Ammophila breviligulata*) and refrigerated. Samples were transported to the University of Houston. Midges were kept frozen and the soil samples were homogenized and refrigerated until we established the experiment.

Plant preparation

We chose the grass *C. longifolia* as the plant species in our experiment. *Calamovilfa longifolia* is one of the most abundant plant species on Lake Michigan sand dunes (Lichter 1998). At Sleeping Bear Dunes National Lakeshore, the grass makes up an average of 40% of the plants on the second, third and fourth dunes from the beach (Crawford, unpublished work), where midges tend to congregate (Crawford and Rudgers 2013). Seeds of *C. longifolia* were surface sterilized in a 10% bleach solution for 5 min and germinated in play sand that had been double autoclaved at 121 °C for 60 min, with a 24-h rest period. Seedlings were transplanted into the experimental pots 3 weeks after the seeds were sown.

Experimental design

We conducted a fully factorial greenhouse experiment where we manipulated midges (present, absent) and soil microbes (live, sterile). The live soil treatment consisted of unmanipulated soil collected from Sleeping Bear Dunes National Lakeshore. To create the sterile soil treatment, we autoclaved a portion of the field-collected soil at 121 °C for 60 min twice, with a 24-h rest period. To help control for differences in nutrients that may be caused by autoclaving, the live and sterile field-collected soils were added to a sterile background soil (10% by volume) composed of autoclaved play sand. The field-collected soil was added to the rooting zone of each plant during transplantation, and was capped with a layer of sterile background soil. We used 170 ml cylindrical pots (Cone-tainers, Stuewe & Sons, Tangent, OR) that were 21 cm tall and had a diameter of 3.8 cm. These pots are suspended in racks, which decreased the possibility of cross-contamination during watering. To establish the midges present treatment, we added approximately 100 midges (estimated by weight) to the top of the soil, mimicking the natural deposition of dead midges in dune vegetation (Fig. 1). The midges absent treatment lacked the midge addition. Each treatment combination was replicated 20 times, for a total of 80 pots. Pots were fully randomized and watered twice a day with 20 ml of water. The plants were not watered for 1 day prior to harvesting.

Responses

To track plant growth, we measured plant height and leaf number once a week, including at the onset of the experiment. After 8 weeks, we harvested above- and belowground plant biomass, dried it to constant weight at 60 °C and weighed it. To determine if our treatments influenced soil nutrients, we sent 40 g of soil from five randomly selected pots per treatment combination to Michigan State University's Soil and

Plant Nutrient Laboratory (East Lansing, MI, USA) for analysis of soil pH and available P, K, Ca, Mg, NO_3^- and NH_4^+. We also sent a single 9.9 g sample of bulk midges for nutrient analysis. Using the same five randomly selected pots from the nutrient analyses, we tested if midges influenced soil moisture by drying 12 g of soil at 60 °C for 48 h, measuring soil dry weight and calculating percent soil moisture. We assessed whether AM fungi colonized plant roots by rehydrating roots from three randomly selected pots from each treatment group for 1 week. From the rehydrated roots, 0.1–0.2 g of the roots were packed into tissue cassettes and stained with 0.05% trypan blue following common procedures (Crawford *et al.* 2020). We mounted the stained roots on microscope slides and quantified the frequency of occurrence of AM fungal structures (hyphae, arbuscules, vesicles) in 60 non-overlapping views observed at 400× magnification.

Statistical analyses

We tested how our treatments influenced aboveground, belowground and total biomass of *C. longifolia* using general linear models with the fixed effects of midge treatment (present, absent), soil microbe treatment (live, sterile) and their interaction (Proc GLM, SAS 9.4). We excluded data from three plants that died during the experiment and two plants that were accidentally a different species. Prior to analysis, we log-transformed biomass measures. We were also interested in whether treatment effects differed over time. Using the data from the last survey of plant height and leaf number, we developed an allometric equation (fit through the origin to remove the possibility of negative values for estimated biomass) relating plant traits to plant biomass: total biomass = 0.00096 × height × leaf number. Our allometric equation explained 94% of the variation in plant biomass. We used the equation to estimate *C. longifolia* biomass for each weekly survey. We analyzed estimated biomass using repeated measures mixed models with the fixed effects of midge treatment, soil microbe treatment, time and all possible interactions (Proc MIXED, SAS 9.4). As before, we excluded data from the five plants that died or were a different species and log-transformed estimated biomass.

To determine how our treatments influenced soil properties, including nutrients, pH and soil moisture, we used general linear models with the fixed effects of midge treatment (present, absent), soil microbe treatment (live, sterile) and their interaction (Proc GLM, SAS 9.4).

RESULTS

Midges greatly increased the biomass of *C. longifolia* (Table 1; Fig. 2). Midges increased aboveground biomass by 347%, belowground biomass by 390% and total biomass by 370%. The positive effect of midges on plant performance appeared quickly. By Week 2 of the experiment, midges increased plant biomass by 61% (Table 2; Fig. 3). The positive effects of midges continued to increase through Week 5 of the experiment, and then they began to level off (Table 2; Fig. 3).

Soil microbes weakened the positive effect of midges on plant performance (Table 1; Fig. 2). In the absence of soil microbes, midges increased aboveground, belowground and total biomass by 598%, 646% and 624%, respectively. However, in the presence of soil microbes, presence of midges, the increases in biomass were 186%, 232% and 211%, respectively. This effect was caused by a combination of microbes promoting plant growth in the absence of midges and decreasing plant growth in the presence of midges (Fig. 2). The interactive effect of midges and soil microbes remained constant over time (Table 2; Fig. 3).

Relative to the soils in the experiment, our single sample of bulk midges had a much lower pH and greater amounts of all nutrients (Table 3). These data should be interpreted cautiously because we did not measure nutrients in multiple bulk midge samples. Despite midges appearing to have greater amounts of nutrients, the addition of midges to the soils did not translate to a large difference in soil properties among treatments. The addition of midges lowered soil pH, and there was a trend for midges to increase soil NO_3^-. Observation of plant roots revealed no evidence of root colonization by AM fungi in any of the treatments.

DISCUSSION

As we predicted, the carcasses of lake emergent midges positively influenced the performance of a dominant dune grass, *C. longifolia*. The decomposing midges, which likely contained relatively high levels of nutrients, may be an essential nutrient addition to otherwise nutrient-poor sand dunes (Lichter 1998; Olson 1958). However, the presence of soil microbes weakened the positive effect of midges

Table 1: Results from general linear models testing how midges (present, absent) and soil microbes (live, sterile) influenced plant biomass

		Aboveground biomass		Belowground biomass		Total biomass	
	d.f.	*F*	*P*	*F*	*P*	*F*	*P*
Midges	1, 74	158.63	**<0.0001**	183.35	**<0.0001**	202.28	**<0.0001**
Soil microbes	1, 74	0.01	0.92	0.69	0.41	0.18	0.67
Midges × soil microbes	1, 74	13.60	**0.0004**	9.79	**0.003**	13.61	**0.0004**

Bold *P* values were significant at $P < 0.05$.

on plant biomass, suggesting that belowground communities may compete with plants for aquatic–terrestrial subsidies. Together, our results show that understanding the effects of aquatic–terrestrial subsidies on plants requires incorporation of the complex biotic interactions in which plants are embedded.

In the presence of midges, soil microbes decreased plant performance, possibly because the microbes competed with plants for the nutrients in midges. Over short timescales, soil microbes tend to outcompete plants for nitrogen sources due to their rapid growth rates, the low diffusion of nitrogen through soil and their high surface-area-to-volume ratios (Jacoby *et al.* 2017; Kuzyakov and Xu 2013; Rosswall 1982). Additionally, soil microbes may uptake and release nitrogen rapidly during microbial turnover, essentially causing nitrogen availability boom and bust cycles every few days (Kuzyakov and Xu 2013). Plants, on the other hand, uptake nitrogen in small amounts, making nitrogen uptake in plants is a longer, more continuous process (Kuzyakov and Xu 2013; Ma *et al.* 2020). Competition between plants and soil microbes for nutrients may be particularly intense in the rhizosphere (Kuzyakov and Xu 2013; Richardson *et al.* 2009) or when plant and soil microbial demand for nitrogen is aligned. In many ecosystems, including temperate and alpine forests, nutrient amendments are decoupled with seasonal plant demand. For example, leaf litter in the fall is available for use and sequestration by microbial communities, and then more slowly released as plant demand increases in the spring and summer (Kuzyakov and Xu 2013). In the case of midge amendments, midge emergence and deposition occurs in early spring, aligning with microbial growth and plant emergence and regrowth. Thus, microbial and plant demand for newly added nutrient sources is co-occurring, creating increased potential for competition between microbes and plants. While competition for nutrients between plants and microbes is a likely mechanism for the decrease in plant performance when soil microbes were present, we cannot exclude other potential mechanisms. For example, the addition of a nutrient-rich resource may have shifted the composition of microbial communities or the outcome of individual plant–microbe interactions. The addition of midges may also have caused the accumulation of microbial metabolites detrimental to plant growth. Experiments that measure the response of microbial communities, including their metabolites, and track the flow of midge-derived nutrients could help resolve the underlying mechanisms.

In the absence of midges, soil microbes slightly increased plant performance. Soils contain diverse communities of microbes, including plant pathogens and plant mutualists. In primary successional ecosystems, like Lake Michigan sand dunes, plant associations with soil mutualists may be particularly important for helping plants cope with stressful environments (Lau and Lennon 2012; Rodriguez and Redman 2008; Smith and Read 1998). Previous work in this system has found mixed effects of soil microbes on plant growth. In an experiment that introduced natural soil inocula to plants in the field, soil microbes (presumably AM fungi) increased the performance of a dominant grass species, *A. breviligulata* (Emery and Rudgers 2011). In a greenhouse study, soil communities extracted from the dunes had no effect on the performance of eight different plant species, including *C. longifolia* (Sikes *et al.* 2012). Our results suggest that whether or not soil microbes influence plant performance may depend on the presence of aquatic–terrestrial subsidies. Interestingly, the effects of microbes do not appear to be driven by AM fungi in our experiment, as we did not detect AM fungi in plant roots (however we note that drying roots and rehydrating them may have impeded our ability to detect AM fungi). Plant growth promoting bacteria, instead, may be increasing plant performance.

Experiments that characterize the dune microbial community, especially those that test the effects of different components of the community (e.g. Sikes *et al.* 2012) on plant growth with and without midges, could help tease apart what microbes are driving positive and negative effects.

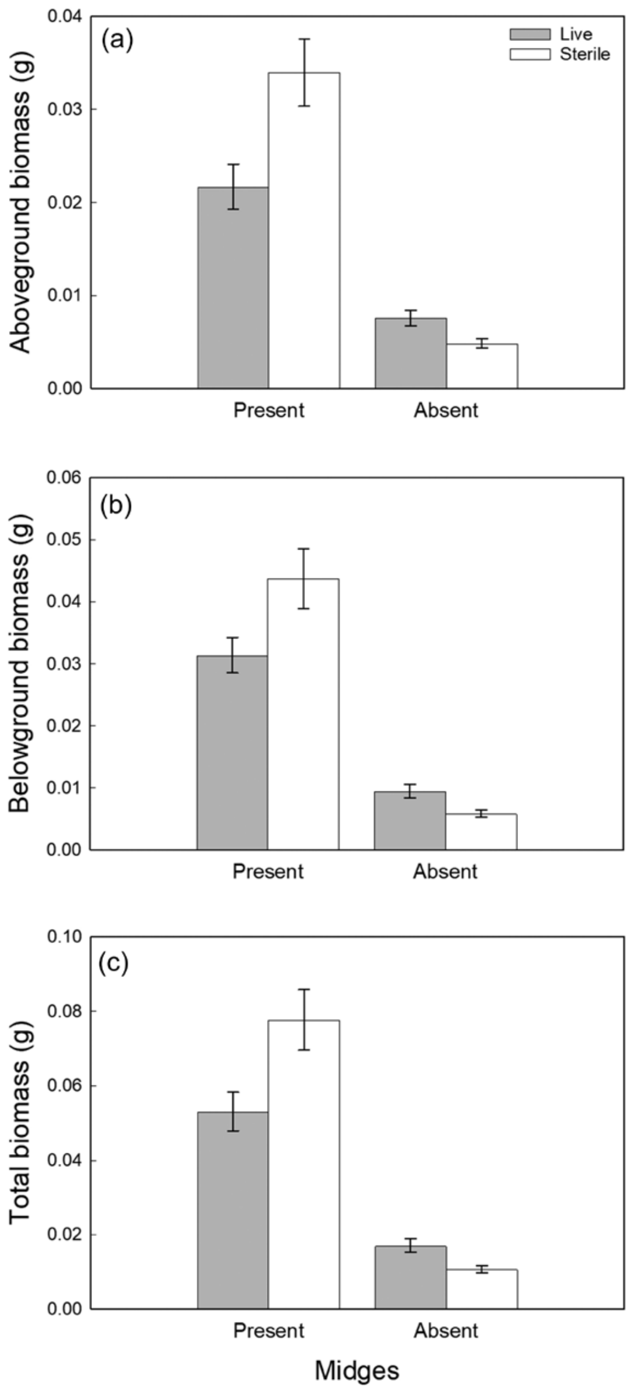

Figure 2: Effect of midges and soil microbes on aboveground (**a**), belowground (**b**) and total (**c**) biomass of *Calamovilfa longifolia*. Bars are average biomass with standard error.

Given their strong effects on plant growth, lake emergent midges may play an important role in structuring communities along the shores of Lake Michigan. In addition to providing resources to consumers, plants on the dunes stabilize sand, creating the structure of the ecosystem (Cowles 1899; Feagin *et al.* 2015). Variation in abiotic and biotic factors, however, could create heterogeneity in midge effects. For example, predation or scavenging of midges by consumers and variation in wind or water flow could increase the patchiness of midge deposition (Dreyer *et al.* 2015). Given the clumpiness of midge deposition (Fig. 1), it is already likely that midges benefit some patches of vegetation but not others. Temperature and climate conditions can also affect the emergence time of aquatic flies (Füreder

Table 2: Results from repeated measures mixed models testing how midges (present, absent), soil microbes (live, sterile) and time influenced estimated plant biomass

	d.f.	*F*	*P*
Midges	1, 71	19.14	**<0.0001**
Soil microbes	1, 71	4.21	**0.04**
Midges × soil microbes	1, 71	16.75	**0.0001**
Time	1, 71	1697.98	**<0.0001**
Time × midges	1, 71	98.04	**<0.0001**
Time × soil microbes	1, 71	2.03	0.16
Time × midges × soil microbes	1, 71	0.05	0.81

Bold *P* values were significant at $P < 0.05$.

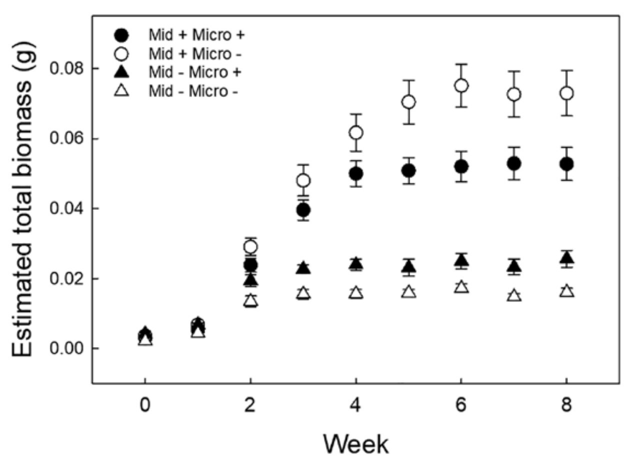

Figure 3: Effect of midges and soil microbes on estimated total biomass of *Calamovilfa longifolia* through time. In the legend, 'Mid' indicates midge and 'Micro' indicates microbes. Points are average estimated total biomass with standard error.

et al. 2005). If midge emergence and plant growth are decoupled, midges may no longer boost *C. longifolia* performance. Finally, there is strong seasonality in dune arthropod community composition, and predators are more abundant than other functional groups (Crawford and Rudgers 2013). Layering in the effects of consumers may weaken the effect of midges on plant growth. To capture the true magnitude of midge effects in this ecosystem, a long-term field experiment with a midge exclusion treatment is necessary (e.g. Hoekman *et al.* 2019). Such an experiment could also help determine the extent of spatial or temporal variation in aquatic–terrestrial subsidies along Lake Michigan.

Midges likely increased plant performance through nutrient subsidies (Bultman *et al.* 2014). Because soil microbes were not necessary for plants to gain benefits from the midges, it is likely that midges hosted microbes that, after their deaths, facilitated the conversion of nutrients to plant-available forms (Osono 2006). It is important to note that after 8 weeks of plant growth we found little difference in soil nutrients among treatments, and our experiment does not allow us to separate increased nutrients from other mechanisms that may lead to increased plant growth in the presence of midges. However, it is unclear what those mechanisms might be. Future experiments could track nutrients and nutrient uptake in plants using stable isotopes to see if plants are incorporating midge-derived nutrients (Dawson *et al.* 2002), and whether the amount of uptake differs in the presence and absence of soil microbes.

Aquatic–terrestrial subsidies can have strong effects on ecosystem structure and functions (Schindler and Smits 2017). However, the impact of aquatic–terrestrial subsidies on individual responses must be considered within the context of the complex interactions that take place within ecological communities (Hines *et al.* 2006). Here, we found that belowground communities, which tend to be understudied relative to other ecological communities, can modify the effect of aquatic–terrestrial subsidies on plant performance. Together, our work shows that understanding ecological interactions can require expanding our focus from discrete communities to incorporate interactions across ecosystem types (e.g. aquatic–terrestrial linkages) and above- and belowground.

Table 3: Effect of midge and soil microbe additions on average soil properties ± SE and soil nutrients from a single sample of bulk midges

Midges	Microbes	pH	P	K	Ca	Mg	NO_3^-	NH_4^+	Soil moisture
Present	Live	8.84 ± 0.02 a	9.60 ± 1.50	16.00 ± 0.71	621.00 ± 30.39	45.40 ± 6.12	0.08 ± 0.04	1.14 ± 0.21	14.5% ± 0.006
Present	Sterile	8.90 ± 0.04 a	7.80 ± 1.66	16.60 ± 0.98	926.60 ± 183.01	53.60 ± 6.71	0.06 ± 0.02	1.12 ± 0.06	13.4% ± 0.007
Absent	Live	9.00 ± 0.03 b	4.00 ± 1.26	16.80 ± 1.11	850.60 ± 85.03	57.60 ± 6.48	0.04 ± 0.02	1.02 ± 0.12	13.0% ± 0.005
Absent	Sterile	8.98 ± 0.02 b	9.40 ± 2.54	18.60 ± 1.08	727.80 ± 141.50	50.20 ± 5.55	0.02 ± 0.02	1.14 ± 0.15	12.4% ± 0.012
Bulk midges		6.1	62	3781	1671	337	6.8	1917	—

Available nutrients are reported in ppm. Letters following values indicate significant differences at $P < 0.05$.

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