



Combined effects of soil heterogeneity, herbivory and detritivory on growth of the clonal plant *Hydrocotyle vulgaris*

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Abstract

Background and aims Fine-scale spatial heterogeneity of soil nutrients often increases growth of plants, especially clonal species. Herbivory could change this positive effect of soil heterogeneity. Furthermore, detritivory may alter soil heterogeneity and indirectly modify herbivory. However, little is known about the interactive effects of soil nutrient heterogeneity, herbivory, and detritivory on plant growth.

Methods We conducted a greenhouse experiment in which we grew the creeping, perennial herb *Hydrocotyle vulgaris* in two soil treatments (homogeneous and heterogeneous) with or without the aphid *Myzus persicae* and with or without the earthworm *Eisenia fetida*.

Results *H. vulgaris* grew more in heterogeneous than in homogeneous soil, even though total nutrient availability

was held constant, and less with than without aphids. The presence of aphids decreased plant growth less in both the high- and the low-nutrient patches in the heterogeneous soil treatment than in the medium-nutrient soil in the homogeneous soil treatment. Earthworms did not affect plant growth but survived better in soil with higher nutrients and in the presence of aphids.

Conclusions Herbivory can increase the positive effects of soil heterogeneity on clonal plants. However, results do not suggest that detritivory modifies effects of soil heterogeneity on plant growth.

Keywords Aphid · Clonal growth · Detritivore · Earthworm · *Eisenia fetida* · Environmental heterogeneity · *Myzus persicae* · Nutrients

Introduction

Both abiotic and biotic factors can cause soil properties, especially soil nutrients, to vary spatially (Alpert and Mooney 1996; Jackson and Caldwell 1993). Such spatial soil heterogeneity is common in natural habitats and frequently occurs on fine scales relevant to plant growth (Liang et al. 2007; Liu et al. 2003). Fine-scale heterogeneity in soil nutrient availability can increase plant growth when the scale of individuals is greater than the scale of nutrient patches (Hutchings and John 2004; Wijesinghe and Hutchings 1999; Wijesinghe et al. 2001). Individual plants can then concentrate roots where nutrient availability is high and benefit from greater ability to take up more concentrated soil nutrients (Hutchings and John 2004;

Hutchings et al. 2003). Clonal growth can increase the effective scale of individuals in plants both by promoting lateral, vegetative spread and through resource sharing between connected plants within clones (Dong et al. 2012; Roiloa and Retuerto 2012; Roiloa et al. 2010; You et al. 2014; Wang et al. 2017). Many studies have accordingly shown that clonal plants perform better in more heterogeneous soils, even when total nutrient availability is held constant (Birch and Hutchings 1994; Dong et al. 2015; Roiloa et al. 2014; Zhou et al. 2012).

In natural systems, the positive effect of soil nutrient heterogeneity on the growth of clonal plants could be modified by herbivory. Specialist herbivores often selectively attack or perform better on plants with a relatively high nutrient content (Adler et al. 2006; Alpehi et al. 1996; Cherif and Loreau 2013; Pérezharguindeguy et al. 2003; Scheu and Jones 1999). Even generalist herbivores can reduce the capacity of a plant to grow and spread into new patches or within patches. These effects could decrease the benefit of high-nutrient patches to plants. On the other hand, higher nutrient supply can increase the ability of plants to resist herbivory with chemical defenses or to tolerate it through regrowth (Burghardt 2016; Fornoni 2011; Hawkes and Sullivan 2001; Kucharik et al. 2016; Sun et al. 2010; Wise and Abrahamson 2005). This may increase the benefit of access to high-nutrient patches.

Further complexity in the effect of soil heterogeneity on plant growth in natural systems might be introduced through the action of soil detritivores such as earthworms. Earthworms can increase overall nitrogen availability to plants by digesting soil, and may reduce soil nutrient heterogeneity by ingesting soil in a high-nutrient patch and excreting in a low-nutrient patch, or increase soil heterogeneity in a relatively uniform soil through excretion (Araujo et al. 2004; Knowles et al. 2016; Lv et al. 2016; Rossi et al. 1997; Shuster et al. 2001). This may indirectly affect herbivory via plant nutrient content (Bonkowski et al. 2001; Scheu and Jones 1999; Wurst 2010; Wurst et al. 2003). For example, earthworms can reduce the reproduction of the aphid (*Rhopalosiphum padi*) on wheat (*Triticum aestivum*) through decrease in nitrogen uptake (Ke and Scheu 2008). Other mechanisms of complex interactions between detritivores, plants, and herbivores include chemical defense. For instance, earthworms have been found to reduce the reproduction of the aphid *Myzus persicae* on *Plantago lanceolata* through indirect promotion of accumulation of iridoid glycosides,

secondary metabolites known to deter generalist insect herbivores and pathogens (Wurst et al. 2003).

To test the combined effects of herbivory, detritivory, and soil heterogeneity on the performance of clonal plants, we conducted a greenhouse experiment with a widespread, creeping, perennial herb in which we crossed the presence and absence of a common herbivorous insect, a common earthworm, and soil heterogeneity. We predicted that soil heterogeneity in the absence of herbivory and detritivory would promote accumulation of biomass by the plant and that herbivory and detritivory would modify the effect of heterogeneity on plant growth, both individually and interactively. We also tested whether soil heterogeneity and herbivory affected the performance of earthworms but made no specific predictions about these effects.

Materials and methods

Species

Hydrocotyle vulgaris L. (Araliaceae, common marsh pennywort, hereafter “*Hydrocotyle*”) is a perennial herb native to moist to wet habitats across much of Europe and parts of northwestern Africa (Murphy et al. 1990). The species was introduced to China as a garden plant in the 1990s and spread into natural habitats from artificial wetland (Miao et al. 2011). *Hydrocotyle* is considered potentially invasive in China because of its rapid clonal reproduction and high phenotypic plasticity (Ma 2013; Miao et al. 2011). The creeping stems bear peltate leaves on long petioles and root at the nodes, which thus function as ramets (Dong et al. 2015). Plants were collected on 10 May 2015 at the Xixi Wetland in Hangzhou, Zhejiang Province, China, and propagated vegetatively in a greenhouse at Forest Science Co., Ltd., of Beijing Forestry University in Beijing, where the entire study was conducted.

Myzus persicae Sulzer (Aphididae, green peach aphid, hereafter “aphid”) is a very widespread, small, euryphagic, piercing and sucking insect that infests a wide variety of agricultural crops and other plants in China and many other countries (Fenton et al. 1998; Li et al. 2015). Parthenogenetic reproduction and short generation time allow individuals to multiply rapidly, and effects of infestation on the host plants include chlorosis, necrosis, wilting, stunting, and malformation of new growth (Goggin 2007). Aphids can also divert host resources to

their feeding sites, reducing growth elsewhere in the plant (Girousse et al. 2005; Sandström et al. 2000). Aphids were collected in the greenhouse in 2015 on plants of *Rosa chinensis* Jacq. and cultured on *Hydrocotyle* for approximately one year until use. The aphids used in the study belonged to a single clone.

Eisenia fetida Savigny (Lumbricidae, redworm, hereafter “earthworm”) is one of the most common earthworms in the world (Aira et al. 2006; Gunadi and Edwards 2003). It is native to Europe but has been intentionally or unintentionally introduced to every other continent. In China, the species is widespread in commercial composting sites, semi-natural grassland, and arable land in Beijing, Heilongjiang, Xinjiang, Jilin, and Sichuan Provinces (Cao et al. 2006; Tiunov et al. 2006); expansion to the north is limited by winter cold. Individuals are about 6 to 8 cm long and live in the upper soil. Earthworms were collected from Shunyi, Beijing, China.

Experimental design

The experiment used a fully factorial design consisting of two aphid treatments (present and absent) crossed with two earthworm treatments (present and absent) crossed with two soil treatments (homogeneous and heterogeneous). Each of the eight combinations of treatments was replicated six times. Replicates were containers 50 cm long by 50 cm wide by 15 cm deep planted with a stem of *Hydrocotyle* approximately 10 cm long bearing two rooted nodes, one fully expanded leaf, one or two immature leaves, and an apex. The average initial stem length was 9.8 ± 0.4 cm (mean \pm SE, $n = 8$).

In the heterogeneous soil treatment, a low-nutrient patch was created by filling half (50 cm long \times 25 cm wide \times 15 cm deep) of each container with 15 L of an 8:2 (v: v) mixture of nutrient-poor loam and commercial potting soil. The loam was collected 10–50 cm below the surface of uncultivated land in Xianghe, Langfang, Hebei Province, China, on 10 July 2016 and sieved through a 2-cm mesh. The potting soil was purchased from Meishimei Bio-Tech Co. Ltd., Beijing, China. To create a high-nutrient patch, the other half (50 cm long \times 25 cm wide \times 15 cm deep) of each container was filled with 15 L of a 2:8 mixture of the loam and the potting soil. The low-nutrient patch contained 0.144% N and 2.20% C; the high-nutrient patch contained 0.598% N and 9.83% C, as measured in samples sent to the Institute of Botany, Chinese Academy of Sciences. In the homogeneous soil treatment, each of the two halves

(patches) of each container was filled with 15 L of an 1:1 (v:v) mixture of the loam and the potting soil. The total amount of soil nutrients was thus the same in the two soil treatments. A plant of *Hydrocotyle* was placed in each container with the stem along the line between the two patches, the distal end of the stem at the edge of the container, and the apex pointed toward the middle of the container. While manipulating nutrient levels by adding fertilizer might have better isolated the effect of nutrients, manipulating nutrient levels by changing the proportions in soil mixtures may better simulate natural heterogeneity; both approaches have been widely used in studies on clonal plants (e.g. Wijesinghe et al. 2001; Zhou et al. 2012; Keser et al. 2014; Wang et al. 2017).

For the treatment with aphids present, eight aphids were released on the mature leaf of the plant of *Hydrocotyle*. The container was covered with a gauze cage 25 cm high to prevent spread of aphids between containers. For the treatment with earthworms present, 30 earthworms were distributed evenly on the soil surface in each container; this provided a density of 100–120 individuals/m², within the range of common densities in arable soils (Cao et al. 2006). The initial length of the earthworms was 5.86 ± 0.08 cm (mean \pm SE, $n = 10$).

Plants were added to containers on 27 July 2016 and allowed to establish for 11 days. Aphids and earthworms were added on 7 August and treatments continued for 51 days. Plants and earthworms used in the experiment were randomly assigned to the treatments. The experiment was conducted in the greenhouse described above. Mean temperature and relative humidity in the greenhouse during the experiment were respectively 28.4 ± 0.3 °C and $64.4 \pm 0.8\%$, as measured by iButtons (DS1923; Maxim Integrated Products, Sunnyvale, CA, USA). Enough tap water was added every three days to keep the soil moist.

Measurements and data analysis

On 27 September, plants and earthworms were harvested separately from each half of each container. In the heterogeneous treatment, halves corresponded to the high and nutrient patches in a container. Plants were first measured for number of nodes (i.e., ramets) and total length of stems. Plants were then divided into roots, stems, and leaves; dried at 75 °C for 48 h; and weighed. Earthworms were counted and weighed.

We used four-way, repeated-measure ANOVAs to test the effects of aphids (present or not), earthworms (present or not), soil heterogeneity (homogeneous or

heterogeneous), and half of container (referred to as “patch”) on number of ramets, total length of stems, and stem, leaf, root, and total mass of *Hydrocotyle* and number of earthworms. Half of container corresponded to high or low nutrient patch in the heterogeneous treatment. In the homogeneous treatment, the two halves did not differ in nutrient level but were compared for purposes of analysis to high and low nutrient patches in the heterogeneous treatment based on position; for example, the left halves of the containers in the homogeneous and heterogeneous treatments with the same aphid and earthworm treatments in the same replicate were compared to each other. Aphids, earthworms, and heterogeneity were treated as fixed effects, and patch as a repeated measure. Differences between individual means were tested with linear contrasts based on ANOVA. Analyses were conducted using SPSS 22.0 (SPSS, Chicago, IL, USA).

Results

Across all other treatments, *Hydrocotyle* accumulated more dry mass and ramets in the heterogeneous than in the homogeneous soil treatment, and in the treatment without than with aphids (Fig. 1, Table S1). Although interactive effects of soil heterogeneity and aphids were not evident in ANOVA tables (Table S1), post hoc contrasts between individual means indicated that the negative effect of aphids on *Hydrocotyle* was less in the heterogeneous than in the homogeneous soil treatment (Fig. 1), especially with regard to shoot growth.

Without aphids, *Hydrocotyle* grew least in the low-nutrient patches and most in the high-nutrient patches in the heterogeneous treatment (Fig. 2); the growth was intermediate in the homogeneous treatment, where nutrient concentrations were intermediate between low- and high-nutrient patches. With aphids, *Hydrocotyle* again grew most in the high-nutrient patches but

Fig. 1 Effects of aphids and soil heterogeneity on mean + SE of (a) total mass, (b) number of ramets, (c) stolon length, (d) stem mass, (e) leaf mass, and (f) root mass of *Hydrocotyle vulgaris* per container. The symbol above a pair of bars shows *P* (linear contrast based on ANOVA): ns > 0.1 ; # $- 0.05-0.1$; * $- 0.01-0.05$; ** $- 0.001-0.01$. See Table 1 for ANOVAs

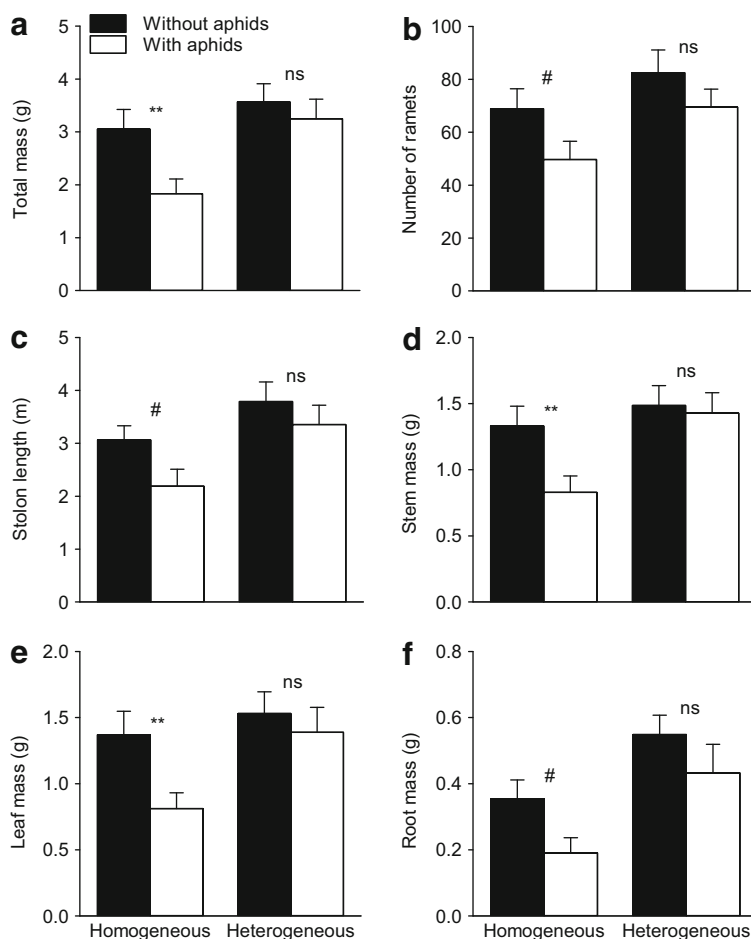
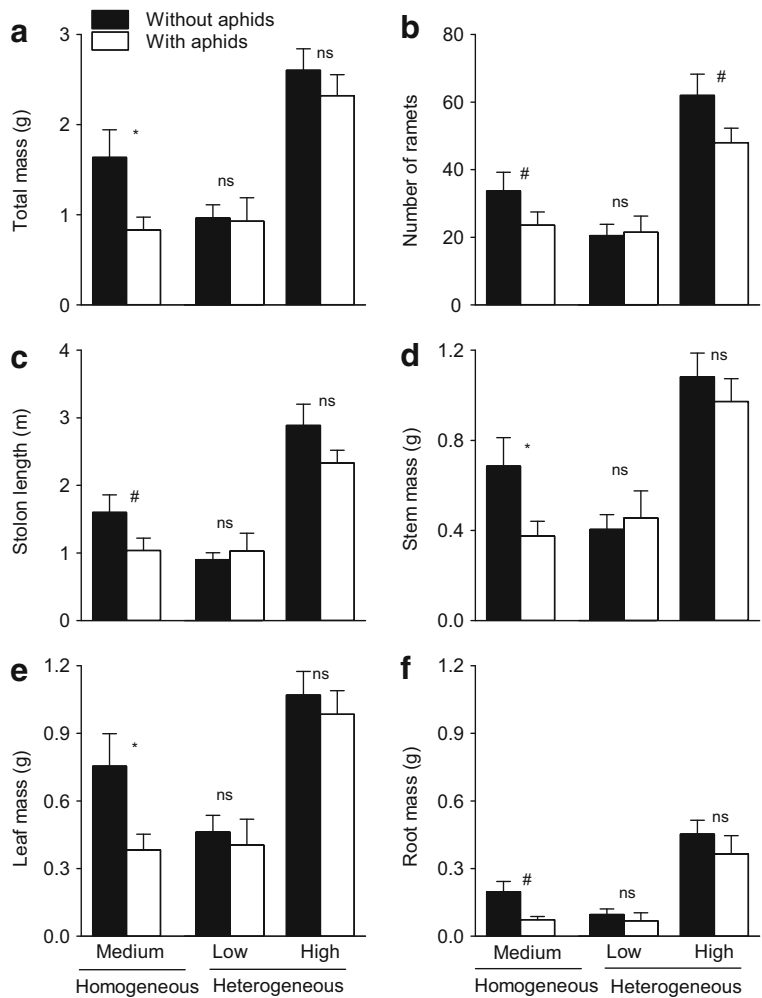


Fig. 2 Effects of aphids and soil heterogeneity on mean + SE of (a) total dry mass, (b) number of ramets, (c) stolon length, (d) stem mass, (e) leaf mass, and (f) root mass of *Hydrocotyle vulgaris* within the low- and high-nutrient patches in the heterogeneous soil treatment and within a randomly chosen half of the container (medium-nutrient patch) in the homogeneous soil treatment. The symbol above a pair of bars shows *P* (linear contrast based on ANOVA): ns - $P > 0.1$; # - 0.05-0.1; * - 0.01-0.05. See Table 1 for ANOVAs



accumulated similar amounts of mass and ramets in the low-nutrient patches and the homogeneous, medium-nutrient treatment. Effects of aphids on accumulation of mass were greater in the homogeneous treatment than in either the low- or the high-nutrient patches in the heterogeneous soil treatment.

As expected, the growth of *Hydrocotyle* did not differ between halves of a container in the homogeneous soil treatment, but was much greater in the high-nutrient than in the low-nutrient side of containers in the heterogeneous soil treatment (Fig. 3; Table S1). The presence of aphids had little effect on these patterns, except

Fig. 3 Differences (mean + SE) between patches within containers with or without aphids in (a) total dry mass and (b) number of ramets of *Hydrocotyle vulgaris*. Difference is high-nutrient minus low-nutrient patch in the patchy treatment and right minus left half in the homogeneous treatment

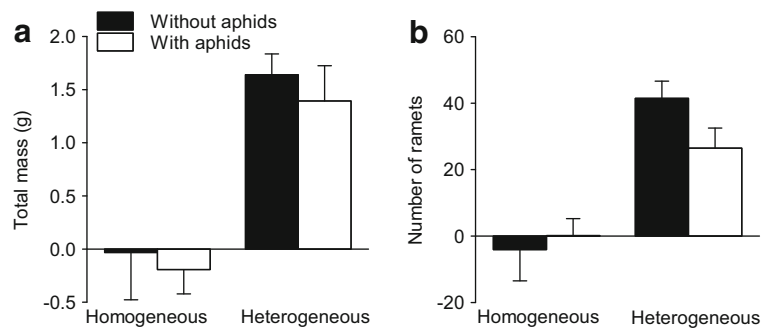


Table 1 ANOVAs of effects of aphids, soil heterogeneity, and patch on total fresh mass and number of earthworms, *Eisenia fetida*

Effect	Fresh mass	No. of individuals
Between-subjects:		
Aphid (A)	14.20*	10.56**
Heterogeneity (H)	6.85*	7.93*
A × H	0.65 ^{ns}	0.75 ^{ns}
Within-subjects:		
Patch (P)	32.50***	58.09***
P × A	0.29 ^{ns}	0.05 ^{ns}
P × H	19.10***	48.29***
P × A × H	0.84 ^{ns}	0.81 ^{ns}

Values are $F_{1,20}$. Symbols give P : ns - > 0.1; * - 0.05-0.01; ** - 0.001-0.01; *** - <0.001

possibly to decrease difference in ramet production between high- and low-nutrient patches.

The presence of earthworms did not affect the growth of *Hydrocotyle* (Table S1). However, aphids and soil treatments affected earthworms (Table 1). Final fresh mass and the number of earthworms were higher in soil with higher nutrients, and higher when aphids were present than when they were not (Fig. 4). The final number of earthworms was about one-third of the initial number of earthworms added, and mean mass per individual did not appear to differ greatly between treatments.

Discussion

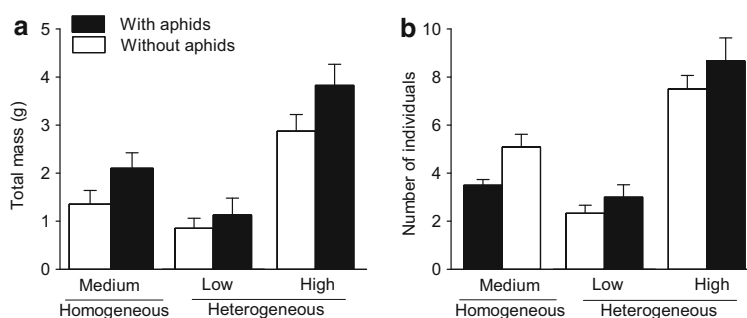
The most interesting result was that the negative effect of herbivory on final dry shoot mass of *Hydrocotyle* was less in heterogeneous than in homogeneous soil, and less in both the high- and low-nutrient patches than in the medium-nutrient soil in the homogeneous treatment.

One possible explanation for a relatively low effect of herbivory in the low-nutrient patches is that aphids performed less well on plants grown on soil with lower nutrients (because the plants were less nutritious or abundant) and so consumed the least plant mass on the low-nutrient patches (Molinari and Knight 2010; Pérezharguindeguy et al. 2003). On high-nutrient patches, aphids might have had relatively little effect on final plant mass because high nutrient availability enabled plants to compensate for herbivory with growth despite relatively high consumption by aphids (Burghardt 2016; Endara and Coley 2011; Stieha et al. 2016).

More generally, this result shows that the positive effects of soil heterogeneity on clonal plants can be greater in the presence than in the absence of herbivory. This contrasts with some previous reports that root herbivory may reduce the positive effect of soil heterogeneity because the root herbivores forage more efficiently for roots in high-nutrient soil patches (Stevens and Jones 2006; Tsunoda et al. 2014). However, some earlier studies have hypothesized that the ability of clonal plants to concentrate ramets in less stressful patches in heterogeneous environments can enhance ability to compensate for herbivory (Sun et al. 2010; Wise and Abrahamson 2007). Interactions between soil heterogeneity, herbivory, and clonal growth could have important implications for community composition and diversity. For example, generalist herbivores can promote plant diversity due to preferences for plants with high growth rates or biomass (e.g. Sonnemann et al. 2015). If herbivory favors the clonal plants in a community by increasing their response to soil heterogeneity, this could feedback to herbivore preference and shift the relative overall performances of plant species in a community.

Even in the absence of herbivory, *Hydrocotyle* accumulated more dry mass and ramets when soil nutrients were unevenly distributed than when they were

Fig. 4 Effects of aphids and soil heterogeneity on mean + SE of (a) total fresh mass and (b) number of earthworms in patches within containers



homogeneously distributed, despite the fact that the total amount of nutrients did not vary. This was consistent with previous studies (Birch and Hutchings 1994; Dong et al. 2015; Zhou et al. 2012). A common explanation is that plants can concentrate growth where nutrients are highest and so experience mainly the high-nutrient patches in a landscape of high- and low-nutrient patches (Gao et al. 2012; García-Palacios et al. 2012; Hodge 2010; Hutchings and Wijesinghe 2008). On average, about three-fourths of the ramets of *Hydrocotyle* in a container were located in the high-nutrient patches in the heterogeneous soil treatment.

The final number of earthworms was greatest in the high-nutrient patches, intermediate in the homogeneous soil with intermediate nutrient levels, and least in the low-nutrient patches. Final numbers in all treatments were much less than the initial number added. The effect of higher-nutrient soil was thus apparently to decrease mortality, which was generally high. Since concentration of total nitrogen and total carbon were both higher in the higher-nutrient soil, it likely provided both better nutrition and moister conditions. Earthworm activity depends on these and other factors (Edwards and Bohlen 1996; Fischer et al. 2014; Nuutinen 1992). The low survival of earthworms might explain their lack of the effect on plant growth. The observed positive effect of aphids on earthworms was not expected. One possible explanation is that herbivory reduced shoot mass and thus transpiration, leaving soil moister (Botha et al. 2004; Burd 2002). Another possibility is that the excretions of the aphids increased the nutritional value of the soil for earthworms, either directly or via effect on other soil organisms (Dighton 1978; Grier and Vogt 1990; Milcu et al. 2015; Petelle 1984). A third possible explanation is that aboveground herbivory by aphids increased root exudation (Holland et al. 1996; Gómez et al. 2010; Schultz et al. 2013).

In sum, this first study on how herbivory, detritivory, and soil heterogeneity may interact to affect growth of clonal plants provides evidence that complex interactions in natural systems can modify the benefits of heterogeneity. In particular, this study shows that herbivory may increase the benefits under certain conditions. Further work may show which types of conditions and which characteristics of herbivores and plants determine whether herbivory increases or decreases benefits of soil heterogeneity, add measures of herbivore performance, test possible mechanisms for effects such as changes in plant chemistry or soil microbes, and

examine how competition between plants may affect interactive effects of herbivory and soil heterogeneity. Relatively few studies have investigated how individual traits may affect networks of interactions between multiple trophic levels in communities. Pursuing this approach is likely to advance understanding of both the full ecological consequences of clonal growth in plants and the complex dynamics of communities.

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