

Tests for negative plant-soil feedback effects within a community context

by
Kenneth John Oppon

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Abstract

The coexistence of numerous species despite competing for similar resources remains a central paradox within the field of ecology. Differentiation of species interactions with resources and their environment has been proposed as a mechanism by which species reduce competitive interactions, thus enabling coexistence between potential competitors. Recent investigations within plant communities suggest that negative feedbacks between plants and their soils could be an important contributor to this differentiation. These plant-soil feedbacks occur when plants condition their soils in ways that disproportionately disadvantage their own species members compared to others, creating conditions that could promote coexistence between species. Tests for these negative plant-soil feedbacks have often focused on the effects of plant associated soil microbes, as the accumulation of host-specific soil enemies have often been implicated as the cause of these feedbacks. However, changes to abiotic soil properties could impact biotically driven feedbacks or even drive feedbacks themselves. Moreover, previous feedback studies have primarily focused on population-level changes to soil properties and their subsequent effects, leading to limited understanding of how abiotic soil components and interspecific interactions within communities interact with biotically driven soil feedbacks.

In this thesis, I investigated the presence of negative plant-soil feedbacks within communities by examining the impact of soil origin on community structure. Using a mesocosm experiment with field-collected turfs from 84 communities, I assessed whether community structure would vary when provided with their own soils, soils conditioned by another community, and soils of mixed origin. Additionally, I manipulated the soil composition by growing communities with field soils or with field soil as live inoculants, enabling the isolation

of biotic soil effects to discern the role of soil microbes and abiotic soil properties in plant-soil feedback effects.

I found evidence of negative plant-soil feedback mediated through soil microbiota as communities grown with their own live inocula soils were less even and species rich than communities grown with live inocula from a different community. These findings suggest that soil specialist enemies impact plant growth and could contribute to species coexistence within these communities. Additionally, I observed positive plant-soil feedback for *Bromus inermis*, an invasive species in North American grasslands, which exhibited a significantly stronger growth response to its own soil microbes compared to those from other communities. This positive feedback may be a key factor in preventing the coexistence of *B.inermis* with other species by promoting its competitive advantage through the soil microbiota. However, soil origin did not strongly impact community species richness, evenness or the growth response of *B.inermis* when communities grew with field soils. Thus, while evidence of soil biota mediated plant soil feedbacks was found, other soil components that vary, such as resources and chemistry, appear to have a larger effect size, masking subtle biotic differences. Together, these findings suggest that plant-soil feedback driven by soil microbes may not be a principal determinant of species coexistence.

Preface

This thesis is an original, collaborative work between me and Dr. James Cahill. Together, we developed the methods and the conceptual framework for the study. I collected and processed the samples, conducted the statistical analyses, and interpreted the results. While I was responsible for writing the manuscript, I also received assistance from ChatGPT. Dr. James Cahill helped refine the final version of the manuscript. No part of this thesis has been previously published.

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Introduction

The assembly of individual plant species as members within local communities is influenced by both regional and local processes. The species pool, comprised of the potential colonizers, is shaped by historical events and the species' evolutionary history (Zobel 1992, HilleRisLambers et al. 2012). However, membership within local communities is determined by a mix of stochastic and deterministic factors (HilleRisLambers et al. 2012). While species dispersal to local areas can be the result of stochastic events and forces (Zobel 1992), deterministic factors such as resource availability and biotic interactions similarly impose restrictions on establishment within local communities (van der Heijden et al. 1998, Reynolds et al. 2003). Even so, the ability of species to coexist stably within communities is suggested to occur when there is sufficient dissimilarity in ecological niches, ensuring that intraspecific not interspecific limitations are greatest for essential resources (Hardin 1960). Recent developments identify that plants establish feedback loops with various soil components (Ehrenfeld et al. 2005) and some suggest that these feedbacks exert great influence on species' growth and survival rates (Chesson 2000). Understanding these feedbacks may be vital to clearly identify the factors influencing the assembly and coexistence of plant species within local communities.

Through the selective depletion of soil mineral nutrients, inputs of decaying plant material, and the release of root exudates, plants modify the abiotic and biotic properties of the soils they inhabit (Hinsinger et al. 2003, Ehrenfeld et al. 2005, Chapman et al. 2006, Bennett and Klironomos 2019). Feedback loops between plants and their soils arise when plant induced changes to soil properties influence whether soil conditions become more or less suitable for current and future occupancy by members of the same species (Bever 1994, van der Putten et al. 2013). In some cases, plants modify soil properties to their advantage resulting in greater growth

and survival in soils previously occupied by themselves (Teste et al. 2017, Bennett and Klironomos 2019). However, overwhelmingly studies indicate that species are subject to negative plant-soil feedbacks (Kulmatiski et al. 2008, Comita et al. 2014, Lekberg et al. 2018). That is, plant growth and survival rates improve if species are exposed to soils that were not previously inhabited by their own species members (Petermann et al. 2008, Cortois et al. 2016). Such negative relationships to soils could promote coexistence amongst plant species if these harmful soil effects overwhelm any inherent fitness differences between species (Chesson 2000), especially if such plant-soil relationships are widespread amongst community members (Bonanomi et al. 2005). While the majority plant-soil feedback tests have focused on herbaceous plants from grassland systems, similar negative soil feedbacks have been shown with plants from various ecosystems and growth forms (Mangan et al. 2010, Liang et al. 2016, Rutten et al. 2016). Therefore, these negative soil feedbacks may be critical to the coexistence of species in natural communities.

Although species specific depletion of soil resources has been identified as an important determinant of coexistence (Tilman 1982), most plant soil feedback studies have focused on the impact of plant-associated soil microbiota (Bever 1994, Kulmatiski et al. 2008, Hodge and Fitter 2013). This is in part due to some plant and soil resource relationships being more dependent on site characteristics (Bezemer et al. 2006) whereas the relationships between plants and soil organisms are known to be tightly coupled with various soil organisms, ranging from antagonists to mutualists (Van der Putten et al. 1993, Packer and Clay 2000, Teste et al. 2017). The cause of negative plant-soil feedbacks is often attributed to the accumulation of host specific soil enemies within the soil biota (Janzen 1970, Connell 1971, Bever 1994, Reinhart 2012). To assess the impact of these soil biota on plant dynamics, most plant-soil feedback experiments grow juvenile

plants indoors in sterile bulk soils with live field soils as inocula to isolate the effects of soil microbes on plant performance while keeping abiotic soil factors consistent (Pernilla Brinkman et al. 2010). However, this inocula approach may mask interactions between the soil microbiota and the abiotic soil properties and their subsequent impact on plant growth (De Deyn et al. 2004, Larios and Suding 2015, Revillini et al. 2016). This approach could also limit the detection of soil feedbacks if they are driven by changes to nutrients or other physiochemical properties of their soils (Chapman et al. 2006, Bonanomi et al. 2008, Ayres et al. 2009, Mehrabi et al. 2015).

Most studies investigating plant-soil feedbacks have only examined these dynamics at the individual and population levels (Kulmatiski et al. 2008, Comita et al. 2014, Anacker et al. 2014, Crawford et al. 2019). Experiments that have integrated interspecific plant-plant interactions reveal a wide range of effects on plant-soil feedbacks. Some species' negative soil feedbacks responses remain unchanged with interspecific interactions (Maron et al. 2016), others exhibit negative soil feedbacks only in the presence of such interactions (Yelenik and Levine 2011, Hol et al. 2013). Alternatively, some species' negative soil feedbacks disappear altogether with interspecific interactions (Casper and Castelli 2007). The exact impact of interspecific interactions on plant soil feedbacks have also been shown to depend on neighbour density and identity (Callaway et al. 2003, Lekberg et al. 2018, Huangfu et al. 2022). Thus, to accurately determine whether species are subject to negative plant-soil feedbacks within their communities requires accounting for the social contexts they are likely to encounter within their local communities (Casper and Castelli 2007).

If negative plant-soil feedbacks facilitate species coexistence, evidence of such effects should be detected when plants are exposed to soils of different origins whilst grown in the social contexts they are often found in their local communities. Communities exposed to soils from

different community origins, should reveal their lowest levels of primary productivity with soils from their own community due to greater accumulation of the species specialist enemies in such soils. In contrast, communities should be most even when exposed to their home soils as fitness differences between community members are more likely to be equalized in home soils due to the presence of their respective soil specialist enemies (Wubs and Bezemer 2018). Species richness may also be strongly affected by home soils, as the accumulation of specialist soil enemies may affect survivorship within home ranges (Packer and Clay 2000, Comita et al. 2014). The differential effects of home soil conditions on these aspects of community's structure compared to soil from a different community origin may become especially stark, if the two soils originate from compositionally dissimilar communities as this should amplify the contrasting soil conditioning effects (Fitzpatrick et al. 2017). Lastly, if the soil microbiota are the principal drivers of these negative soil feedbacks, similar outcomes should be observed whether communities are provided field soils or field soils as inocula (Klironomos 2002, Anacker et al. 2014).

Methods

Study area

To investigate the impact of soil origin on community structure, I collected soil and turf samples from a 9-hectare section of the Roy Berg Kinsella Research Ranch, located in the Aspen Parkland ecoregion of Alberta, Canada (53°05'0" N, 111°33'0" W). The ranch is a savannah habitat with mixed prairie, *Populus tremuloides* Michx. forests, and shrub-dominated areas (Dettlaff et al. 2018, Peetoom Heida et al. 2021). Prominent grasses in the grassland areas include *Poa pratensis* L., *Festuca hallii* (Vassey), *Elymus trachycaulus* (Link) Gould, *Bromus inermis* Leyss as well as a diverse array of forbs (Brown and Cahill Jr. 2019, Stotz et al. 2019).

There can be considerable changes to species diversity at small scales within these grassland areas (White et al. 2012, Bennett and Cahill 2016, Brown and Cahill Jr. 2019). While species are understood to be co-limited by the availability of nutrients and water (Lamb et al. 2007), they have also been shown to be strongly affected by their associations with soil organisms (Bennett and Cahill 2016). These features make this area ideal to investigate whether plant soil feedback effects are an important structural force to these grassland communities and whether changes to abiotic or biotic soil factors are the principal cause.

Experimental design

A mesocosm experiment was conducted using a reciprocal transplant design to examine the impact of soil origin on community structure. The data from this experiment was then used to determine whether dissimilarity between soil origins impacted soil origin effects on community structure. For the mesocosm setup, pairs of in situ communities (grassland turf) and their soils were collected from 42 randomly chosen sites at the ranch (Table 1; Figure 1). Mesocosms were constructed such that each turf within a pair was exposed to soil conditions they were previously exposed or unexposed to in the field. Turfs were grown with soils that originated from their own turf or from the other turf within the pair, enabling a comparison of home soil effects against other soil origins (Figure 2). The experiment included multiple soil content treatments to differentiate between total soil effects (abiotic and biotic) and biotic effects in isolation. There were two soil content treatments (field soil and live inoculum) crossed with three soil origin treatments (home, away, mixture), replicated for the 42 turf pairs. Additionally, 7 turf pairs had extra mesocosms constructed with sterilized versions of their soil inoculum to assess any non-biotic effects of the inoculum.

Community and soil sampling

The 42 sites were sampled during the early period of the growing season (May 2021). The goal was to collect samples from sites with varying levels of local vegetative dissimilarity within a defined area. The initial aim was to select 12 representative sites for each dissimilarity class (i.e., high, medium, and low dissimilarity). However, due to concerns that community composition could not be accurately assessed *a priori* so early in the growing season, visual assessments of vegetative dissimilarity were relied upon to guide the site selection, rather than a systematic assessment of vegetative composition. The distance between sites varied, but efforts were made to keep sites at least 5m apart (Figure 1). At a given site, a 3m diameter area was marked, and two 0.5 X 0.25 m quadrats were established, ensuring that these were separated by approximately 1m to limit spatial dissimilarity (Figure 1). The turf communities from each quadrat (0.5 x 0.25m) were extracted by shovelling and severing the roots 10-15 cm deep. Turfs were labelled and stored in plastic seed germination trays (0.5x 0.25x 0.06 m) for transport. Soil samples were then collected via shovelling a further 10 cm below the origin of each turf community and by mechanically separating soil from intact turf roots. The shovel was cleaned with ethanol between sample collection from each community. The individual soil samples from each community were homogenized and stored in resealable plastic bags. In total, there were 84 turf communities and soil samples. The turfs and soil samples were then transported to the Biological Sciences Building at the University of Alberta located in Edmonton, Alberta, Canada (53°31'43.9" N, 113°31'34.2" W) until use. Following transport, turfs were divided into separate 5x15 cm labelled segments. Meanwhile, soils were aerated and passed through a 6mm sieve to remove large roots and rock fragments. This process resulted in at least 6 turf segments and sufficient soil from each turf community to allow for the soil x turf transplant experiment. While

the turf transplant approach has the potential to introduce disturbance-related effects to the vegetation, such as transplant shock, an attempt was made to account for this by using vegetation collected early in the growing season. It is also recognized that the individual turf segments from a singular turf community will not be exactly similar, particularly in the context of rare species. However, as segments were randomly assigned to treatments, there is no systemic bias of such variation, and instead, it is part of the ‘noise’ of the study. Thus, aspects of precision are sacrificed for increases in realism.

Rooftop mesocosm experiment

The mesocosms were composed of 20cm diameter pots, approximately 15cm deep, filled with 2.5L of various soil types (Figure 2). Pots were separated into halves using a vertical pot insert. For the home and away soil mesocosms, both halves of the pot were filled with soil collected from a single turf community within a site. Turf segments were grown in their own soil (home), soil from the counterpart turf community within the pair (away), or a 50:50 combination of both soils (mixed). The latter was not a homogenous mixture of the two soil origins, but instead had the soils of different origin separated into the two halves of the pot (Figure 2). There were two volumes of field soils used in the mesocosms (field soil only and field soil as live or sterile inocula). Field soil mesocosms had each half of the pot filled with an undiluted 1.25L of field soil, allowing for identification of total soil effects (Anacker et al. 2014, Kostenko and Bezemer 2020). In the live inocula mesocosms, each half of the pot was filled with a 9:1 ratio of sterilized background soil (1.125L) with field soil (0.125L), allowing the identification of effects specific to the soil microbiota (Chagnon et al. 2018, Werger et al. 2020). The background soil was a low nutrient mix of 3:1 sand and topsoil. A sterilized version of the inocula treatment was constructed by using sterilized field soils in some of the mesocosms. This allowed the

assessment of any non-biotic effects of the inoculum. The low nutrient sand: topsoil mixture and the sterile field inocula samples were autoclaved at 3 hours at 121 °C before use. Pot inserts were removed once both halves were filled.

After the soils were constructed (June 2021), the turf segments were added to the pots so that each turf community within a pair had a segment exposed to one of six different soil types (origin: home vs away vs mixed) x (content: field soil vs inocula). The segments were placed longitudinally in the center region of the pots, straddling the area once occupied by the insert, allowing root access to both portions. These mesocosms were then placed on the southward-facing section of the rooftop at the University of Alberta's Biological Sciences building. Mesocosms were arranged into blocks, with each block comprising of all mesocosms created with segments from the turf communities within a pair collected from a field site. This arrangement aimed to maintain consistency in the environmental conditions vegetation collected from a single field site experienced. The location of individual mesocosms within each block was randomized, and mesocosms were watered twice per day for the duration of the experiment.

Measurements

The mesocosms grew for of 15 weeks as to allow vegetative growth for the duration of the growing season as well as to permit accurate identification of all species within the communities. After this period, mesocosms were harvested to measure shoot and root responses to the soil treatments. Shoots were sorted by species and clipped at the soil surface from each mesocosm, then dried for 48 hrs at 60°C before being weighed. To determine root growth responses to the soil treatments, samples of the root systems from the communities within each mesocosm were collected. Root samples were obtained using two 3.5cm diameter soil cores located approximately 2.5cm from the two longitudinal edges of each turf segment, with each

core being approximately 15cm deep. For the mixed soil mesocosms, a core was taken in the pot region initially filled with soils from the turf segment's own community, and the other core was taken in the pot region filled with soils from the away community. Roots from the cores were washed and dried for 48 hrs at 60°C, then weighed.

Analyses

All analyses were performed in R (R Core Team 2022) with the packages 'emmeans', 'lme4' and 'vegan'. The data were visually inspected to ensure assumptions of normality and homoscedasticity were met. A series of general linear models followed by planned comparisons analyses were conducted to determine how soil origin (home, away, mixed) affected the structure of the mesocosm communities. Community structure was assessed via the net aboveground primary productivity (ANPP), below-ground productivity, species evenness and richness of each mesocosm. Species richness was calculated as the total number of unique species present within the mesocosms and species evenness was estimated as $J' = H/\ln(S)$, where 'H' is the Shannon diversity index and 'S' is the species richness. In all linear models, soil content (field soil, live and, sterile inocula) and soil origin (home, mix, away) were fixed factors, and turf segment origin was the random factor. Mesocosms that had no vegetative production for the duration of the experiment were excluded from all analyses, as those instances were attributed to transplant failure rather than soil effects. Furthermore, some root samples were unable to be accurately assessed and were omitted from the analyses.

The planned comparisons for each linear model were between mesocosms that contained turf segments grown on their own soil (home) and those grown on soil from a different community(away) or those grown on soils of mixed community origin (mixed). These comparisons were conducted only between mesocosms with similar soil contents.

To determine species-level responses to soil origin, a natural log response ratio was calculated for the species that were present in both turf segments used to construct home and away soil mesocosms for an individual turf. The mean of a species' response ratio across all turf communities was calculated and then tested for significance against zero using a one-sample t-test. The species-specific response ratio for each turf was calculated using the formula, $\ln(\text{Home}/\text{Away})$. In this context, "Home" represents the aboveground biomass of a given species in a mesocosm with a turf segment growing in its own soil, and "away" represents the species aboveground biomass in the separate turf segment of similar origin but now growing in soil collected from the other turf community within its turf pair. Separate species response ratios were calculated for each of the soil content treatments, resulting in three mean response ratios. Only species with mean response ratios across all three soil content treatments were included in the analysis as to accurately pinpoint the soil component responsible for any significant growth responses to soil origin. In total, eight species found within our mesocosm communities met this criterion.

To determine how turf dissimilarity within each pair impacted the soil origin effects on community structure, site-specific natural log response ratios were calculated from all mesocosm community structure metrics. These response ratio values were then regressed against the Bray-Curtis dissimilarity values calculated between the turfs within each pair collected at each field site to determine the relationship between all community metric response ratios and turf dissimilarity. The site-specific response ratios were calculated using the formula $\ln(\text{Home}/\text{Away})$. In this context, 'Home' represents either the combined aboveground net primary productivity (ANPP), species richness, or species evenness value from both home soil mesocosms constructed with segments from the turf community pair from an individual site.

'Away' represents the combined ANPP, species richness, or species evenness values from both away soil mesocosms constructed with turf segments from the same turf pair. Positive response ratio values indicate a greater benefit of home soil than away soil conditions for a given community metric, whereas negative response ratio values indicate a greater benefit of away soil conditions. The absolute values of each site-specific response ratio were also calculated and then regressed with the Bray-Curtis dissimilarity values to determine if a relationship exists between the effect size of response ratios and the dissimilarity of the turf communities. Separate site-specific response ratios were calculated for the mesocosms with field soil and live inocula soils. Response ratios were not calculated for sterile inocula mesocosms due to limited replication across sites. Transplant failures meant that field soil response ratios could not be calculated for two sites.

The dissimilarity between the turf communities within a pair from each site was assessed through an analysis of species composition differences. Relative abundances of species within each turf community were calculated, and these data were utilized in a Bray-Curtis analysis to determine compositional dissimilarity between pairs. The dissimilarities between each turf, based on the relative abundances of their respective species, were ordinated using a Principal Coordinate Analysis (Figures 3 and 4). A cailliez transformation was applied to the dissimilarity data prior to ordination. This method of ordination was selected due to its ability to provide the best data representation with the fewest dimensions.

The relative abundances of species within each turf community were derived from the mesocosm experiment, as it was not feasible to perform an a priori assessment of these turf communities' composition. To calculate a turf's productivity, the ANPP of all home soil mesocosms, irrespective of their soil content, that were established with segments from the

respective turf was aggregated. Some species that were absent at the field sites but present in certain mesocosms (Table 8) were likely introduced through seed rain during the experiment. However, these occurrences were relatively infrequent and made minor contributions to the overall community structure; therefore, they were not excluded from the analyses. The relative abundance of each species within a turf was determined by calculating their contributions via shoot biomass to the aggregated ANPP across all the home soil mesocosms for that specific turf.

Results

While there was a main effect for soil content in the linear mixed model for aboveground net primary productivity ($F_{2,475.19}=37.81, p<0.001$; Table 2) and belowground productivity ($F_{2,451.06}=13.90, p<0.001$; Table 2), there was no main effect of soil origin on aboveground net primary productivity ($F_{2,450.33}=0.058, p=0.943$; Table 2) or belowground productivity ($F_{2,431.41}=0.281, p=0.754$; Table 2). Similarly, while there was a main effect of soil content in the linear mixed model for species richness ($F_{2,465.51}=31.15, p<0.01$; Table 3), soil origin did not reveal a strong main effect ($F_{2,450.19}=1.444, p=0.237$; Table 3). The linear mixed model for species evenness did not reveal strong main effects for either soil content ($F_{2,471.78}=1.939, p=0.145$; Table 3) or soil origin ($F_{2,450.28}=0.985, p=0.374$; Table 3).

How does soil origin affect plant community productivity?

Our planned comparisons revealed that ANPP in home soils was similar to ANPP in away and mixed soils, and that this was consistent across all three soil content treatments (Table 4; Figure 5). Similarly, planned comparisons found that root biomass in home soils did not differ significantly from that in away soils or mixed soils across all soil content treatments (Table 5; Figure 6)

How does soil origin affect plant community species richness?

Planned comparisons found no difference in species richness between communities with home soils compared to those with away and mixed soils in the field soil treatment (Table 6; Figure 7). In contrast, there were differences in species richness within the live inocula treatment. Communities grown with the live inocula version of their home soils were less species rich than those with away live inocula soils ($T_{1,164} = -0.464, p=0.027$; Table 6; Figure 7) but were not different than those grown with mixed soils ($T_{1,164} = -1.113, p=0.206$; Table 6; Figure 7). There were no significant differences in species richness between communities with home soils and away or mixed soils in the comparisons for sterile inocula (Table 6; Figure 7).

How does soil origin affect plant community evenness?

A similar effect seen in the comparisons for species richness was seen with species evenness within communities. There were no differences between the evenness of home soil communities and those communities grown with away or mixed soils in the field soil treatment (Table 7; Figure 8). The live inocula versions of soils showed that home soil communities were much less even than away soil communities ($T_{1,161} = -2.21, p=0.028$ Table 7; Figure 8) but not mixed soils ($T_{1,159} = -1.56, p=0.121$ Table 7; Figure 8). There were no strong differences in species evenness between home soil communities and the other two soil origins in sterile inocula soils (Table 7; Figure 8).

How do individual species respond to soil origin?

None of the common species within in the mesocosm communities showed strong growth responses to soil origin when grown on field soils as all were similarly productive on home and away soils (Table 9; Figure 9). In live inocula soils, only *B. inermis* showed a strong growth response, with greater shoot productivity on home soils than away soils, consistent with a

positive plant soil feedback ($T_{1,5}=2.640$, $p=0.045$; Table 10; Figure 10). In the sterile inocula treatment, no species showed a strong growth response to soil origin (Table 11; Figure 11).

Soil origin effects and turf compositional dissimilarity

The linear regressions showed that there was no relationship between the compositional dissimilarity of the turf communities within each pair collected across the field sites and the productivity response ratios from their field soil mesocosm communities (Table 12; Figure 12a). However, there was a positive relationship between the compositional dissimilarity of turf communities in each pair and the absolute value of their productivity response ratios from their field soil mesocosm communities ($r^2=0.09$, $p=0.04$; Table 12; Figure 12b). This meant that the more dissimilar the two soil origins were across our field sites, the stronger the relative impacts of home and away field soils had on community productivity. There was a prominent, albeit non-significant, negative trend between the compositional dissimilarity of turf communities in each pair and species richness response ratios of the mesocosm field soil communities ($r^2=0.09$, $p=0.055$; Table 13; Figure 13a) but there was no relationship between compositional dissimilarity and the absolute values of these response ratios (Table 13; Figure 13b). This indicated that the more dissimilar the soil origins were within each turf pair, the more harmful home field soil conditions were to species richness. Another non-significant but prominent trend also emerged between the compositional dissimilarity of the turfs within each pair and their evenness, where the more dissimilar turfs were, the less even communities grown on their home soils were relative to when they grew on away soil conditions ($r^2=0.08$, $p=0.07$; Table 14; Figure 14a) and there magnitude of this effect increased with increased turf dissimilarity ($r^2=0.19$, $p=0.004$; Table 14; Figure 14b). In contrast, there was no relationship between the compositional

dissimilarity of the turf communities within each pair and any of the live inocula mesocosm communities' response ratios or their absolute values (Tables 15-17; Figures 15-17).

Discussion

The mesocosm experiment provided mixed support for negative plant-soil feedbacks as a stabilizing mechanism contributing to coexistence of species within communities. Community productivity, both aboveground and belowground, were unaffected by soil origin, suggesting that most species within these communities were not uniquely affected by soil from their own communities. However, there was a significant reduction in species richness in communities grown with their own soil compared to those grown with another community's soil. This reduction in species richness was specific to the live inocula soil treatment and indicated that certain species might be strongly impacted by the accumulation of soil-specific pathogens within their soil biota, consistent with previous studies (Packer and Clay 2000, Cortois et al. 2016). Nonetheless, there was also evidence suggesting that some species benefited more from the microbes within their own soil biota than those from other communities. This was evident in communities grown on their home soil, which exhibited greater variability in species abundance than those on away soil communities in the live inocula treatment. A notable example was observed with *B. inermis*, which displayed a more pronounced growth response to its home soil microbes than to soil microbes from other communities. Interestingly, there were no apparent strong effects of soil origin on any aspect of community structure or species growth responses in the field soil treatment. This suggests that the abiotic components of field soils, including nutrients, organic matter, and other physiochemical properties, may have moderated the influences of soil-specific organisms (Manning et al. 2008, Kos et al. 2013, Larios and Suding 2015, in 't Zandt et al. 2019). This underscores the intricate interplay between abiotic and biotic

soil factors in shaping plant-soil interactions, as other have suggested (Ehrenfeld et al. 2005, Cortois and De Deyn 2012). In light of these findings, it becomes evident that both aspects of soils—abiotic and biotic—need to be considered simultaneously when investigating plant-soil feedback dynamics..

Since the biotic and chemical properties of the field soils collected and used in this experiment were not examined, it is unclear the specific soil agents responsible or involved in any of the strong soil origin effects detected. There is a precedent that negative soil feedbacks within this system may be driven by soil fungi as their harmful effects on plant growth and survival have been previously reported in a prior study within the area (Bennett and Cahill 2016) and in other temperate grasslands (Bever 1994, Casper and Castelli 2007).

The use of separate turf segments from individual turfs for their respective mesocosm communities means that the absence of a particular species in communities of similar soil content and turf segment origin but different soil origins may not wholly be explained by soil origin effects but may also be attributed to chance. Consequently, it is challenging to pinpoint the precise targets of the negative soil feedbacks contributing to the decrease in species richness within the live inocula home soil communities. Notably, none of the common species within the mesocosm communities exhibited strong negative responses to their home soil biota, suggesting that it may be the rare species that are particularly susceptible to these negative soil feedback effects (Klironomos 2002, Yenni et al. 2012). However, the experiment methodology employed for this study was not well suited to detect soil origin effects on rare species. Therefore, this may be a potential avenue for future research.

While most of the common species within the mesocosm communities were not strongly influenced by soil origin, the majority did show a slight preference for their home soil

conditions. However, only the invasive *B. inermis* reported a prominent preference for home soils, exclusive to the live inocula treatment. This finding is consistent with the notion that positive soil feedbacks contribute to the invasive potential of exotic species within their communities (Klironomos 2002, Callaway et al. 2003, Jordan et al. 2008, Crawford and Knight 2017). Although *B. inermis* changes the biotic diversity of the soil biota during the course of its invasion (Piper et al. 2015), a previous study within this system suggest that this invader modifies the soil biota to its detriment (Stotz et al. 2018). The discrepancy between the finding reported by the previous study and that presented here, can likely be attributed to the different social contexts in which the plants were grown. Stotz et al. reported on *B. inermis*' soil feedback response when grown alone, whereas in this study, the plants grew alongside interspecific neighbours. As others have reported, this change in a plant's social setting can alter the soil feedback species experience (Callaway et al. 2003, Shannon et al. 2012). Therefore, this discovery may highlight the importance of the social context in which *B. inermis* interacts within its communities and how it may be integral to the establishment of positive biotically driven soil feedbacks. As *B. inermis*' preference for home soil was not as prominent in the field soil treatment indicates that abiotic properties impact these soil feedbacks. However, as this study was not intended to investigate the mechanisms of *B. inermis* invasion, more work is warranted to fully understand and substantiate the result reported here.

Despite the mixed nature of the soil origin effects on the structure of the mesocosm communities, consistent evidence emerged, suggesting that the importance of soil origin effects increased as the compositional dissimilarity between turf pairs, from which the soils were collected, also increased. This pattern held true solely for the field soil mesocosm communities, implying that it is the unique modification of abiotic soil properties, rather than the soil biota,

that significantly influences species within this system. The relationship between the compositional dissimilarity of soil origins and their relative impacts on community structure did not offer clear insights into how plant-soil relationships contribute to species coexistence. However, that increasing compositional dissimilarity of soil origins was significant only for the field soil mesocosms suggests a stronger likelihood that if soil feedbacks effects were to materialize within this system, they would be driven by changes in abiotic, rather than biotic, soil properties (McCarthy-Neumann and Kobe 2010, Mehrabi and Tuck 2015, Fitzpatrick et al. 2017, Kuřáková et al. 2018).

Caveats

It is worth noting that among the 24 species-specific tests of soil origin conducted, 23 detected no effect, except in the case of *B. inermis* in live inocula. The overwhelming consistency in species level responses to soils of different origin thus raises concerns whether the effect seen with *B. inermis* in live inocula may have been spurious. Similarly, due to the sheer number of communities, the differences observed in community evenness and species richness for communities grown with live inocula from their own communities and from a separate community may be driven by numerous small differences rather than a singular large effect. Thus, these results are interpreted with a degree of caution.

As the mesocosm communities were established from turf segments, most of our species grew in the presence of competitors, which may have obscured soil-conditioning effects (Casper and Castelli 2007, Crawford and Knight 2017). Moreover, since most of the species in the mesocosm communities were likely established individuals within the turfs, they may be less susceptible to plant-soil feedback effects, especially negative, due to their age (Kardol et al. 2013, Dostálek et al. 2022). Older plants tend to be better defended against enemies (Develey-

Rivière and Galiana 2007, Quintero and Bowers 2011), and this could be especially true for perennials which invest more into defensive traits (Cortois et al. 2016) and dominate this system (Table 8). Moreover, older plants also tend to be less susceptible to resource fluctuations, as they can be more efficient users of soil resources (Pastor-Pastor et al. 2015) especially if they originate from nutrient limited systems. Therefore, soil origin effects may be more evident in the earlier life stages of the species present within this system.

Another important contributor to the similarity of plant productivity across soils of different origins in this study here may be explained by resource availability and the environmental conditions of the experiment. Water availability is a strong determinant of plant productivity within this system (Lamb et al. 2007). Variability among species drought tolerances and water availability could contribute to the feedbacks of some species (Wilschut and van Kleunen 2021). The regular provision of water for the duration of this experiment may have thus obscured these plant soil feedback effects, that may occur naturally. However, outdoor experiments, like this one, have also reported similar plant productivity across soils of different origins (Macel et al. 2007, Schittko et al. 2016, Heinze and Joshi 2018, Kirchhoff et al. 2019, Werger et al. 2020). This suggest that the variable environmental conditions plants experience naturally (Poorter et al. 2016) obscures soil origin effects that could be apparent when plants are exposed to much more environmentally homogeneous conditions. Future efforts could thus be devoted to decoupling these two aspects to determine how resource availability and environmental heterogeneity may have contributed to the findings reported here.

Conclusion

These findings challenge the notion that negative soil feedback effects, particularly those driven by soil biota, are a principal mechanism promoting species coexistence within communities. While evidence indicated that communities were structured differently when exposed to soil biota from different origins, with the impact of host-specific soil pathogens being notable in their home soils, there was also evidence that certain species greatly benefited from the soil biota found in their home communities. Moreover, in the case of communities provided field soils, soil origin appeared inconsequential, suggesting that abiotic soil properties moderated the effects of all soil microorganisms on plant growth and survival. This highlights the need for caution when drawing conclusions from plant-soil feedback studies that exclusively focus on soil microbial effects.

Tables and Figures

Table 1- Sampling sites within the Roy Berg Kinsella Research Ranch located in Alberta, Canada. Sites were sampled in May 2021.

Site	Latitude (N)	Longitude (W)
1	53° 5' 3.59"	111° 33' 31.14"
2	53° 5' 2.15"	111° 33' 26.28"
3	53° 5' 1.54"	111° 33' 25.85"
4	53° 5' 2.51"	111° 33' 25.60"
5	53° 5' 7.54"	111° 33' 31.32"
6	53° 5' 7.54"	111° 33' 32.29"
7	53° 5' 7.37"	111° 33' 33.31"
8	53° 5' 6.65"	111° 33' 33.79"
9	53° 5' 4.13"	111° 33' 37.51"
10	53° 5' 4.17"	111° 33' 37.48"
11	53° 5' 4.05"	111° 33' 34.97"
12	53° 5' 4.22"	111° 33' 34.82"
13	53° 5' 3.33"	111° 33' 35.89"
14	53° 5' 3.44"	111° 33' 35.46"
15	53° 5' 4.91"	111° 33' 29.59"
16	53° 5' 4.66"	111° 33' 29.38"
17	53° 5' 4.09"	111° 33' 29.93"
18	53° 5' 4.05"	111° 33' 29.88"
19	53° 5' 4.73"	111° 33' 29.82"
20	53° 5' 5.08"	111° 33' 27.9"
21	53° 5' 5.14"	111° 33' 35.42"
22	53° 5' 5.29"	111° 33' 33.73"
23	53° 5' 4.66"	111° 33' 33.94"
24	53° 5' 4.77"	111° 33' 36.29"
25	53° 5' 3.66"	111° 33' 36.36"
26	53° 5' 4.03"	111° 33' 33.65"
27	53° 5' 6.59"	111° 33' 36.33"
28	53° 5' 6.45"	111° 33' 36.88"
29	53° 5' 4.74"	111° 33' 37.92"
30	53° 5' 4.94"	111° 33' 37.79"
31	53° 5' 24"	111° 33' 37.66"

32	53° 5' 23.88"	111° 33' 36.73"
33	53° 5' 24"	111° 33' 49.07"
34	53° 5' 24.14"	111° 33' 49.39"
35	53° 5' 24.39"	111° 33' 49.21"
36	53° 5' 24.35"	111° 33' 49.29"
37	53° 5' 24.5"	111° 33' 49.29"
38	53° 5' 24.25"	111° 33' 49.17"
39	53° 5' 8.28"	111° 33' 47.89"
40	53° 5' 8"	111° 33' 47.88"
41	53° 5' 8.09"	111° 33' 47.99"
42	53° 5' 8.64"	111° 33' 45.84"

Table 2- Summary table for the linear mixed models of annual net primary productivity and belowground biomass of mesocosm communities. Soil origin and soil content were fixed factors, and turf origin was the random factor in both models. Df_{den} = Kenward- Roger adjusted denominator degrees of freedom.

		ANPP			Belowground biomass		
Treatment	df	<i>F</i>	df_{den}	<i>P</i>	<i>F</i>	df_{den}	<i>P</i>
Soil origin	2	0.058	450.33	0.943	0.281	431.41	0.754
Soil content	2	37.819	475.19	<0.001	13.905	451.06	<0.001
Soil origin x Soil content	4	0.399	450.22	0.809	1.414	431.16	0.228

Table 3- Summary table for the linear mixed models of species richness and evenness of mesocosm communities. Soil origin and soil content were fixed factors, and turf origin was the random factor in both models. Dfden= Kenward- Roger adjusted denominator degrees of freedom.

Treatment	df	Species richness			Species evenness		
		F-value	df.den	P-value	F-value	df.den	P-value
Soil origin	2	1.444	450.19	0.237	0.985	450.28	0.374
Soil content	2	31.150	465.51	<0.001	1.939	471.78	0.145
Soil origin x Soil content	4	0.906	450.12	0.460	0.985	450.18	0.415

Table 4- Summary table of planned comparisons from the linear mixed model of aboveground net primary productivity of mesocosm communities, where soil origin and soil content were fixed factors, and turf origin was the random factor.

Aboveground net primary productivity (ANPP)					
Contrast	<i>df</i>	Mean difference	SE	<i>t</i> -value	<i>P</i> -value
Home- Away Field soil	165	-0.046	0.122	-0.383	0.701
Home-Mixed Field soil	164	-0.018	0.121	-0.152	0.879
Home - Away Live inocula	164	-0.046	0.149	-0.314	0.753
Home - Mixed Live inocula	165	-0.059	0.15	-0.395	0.693
Home - Away Sterile inocula	26	0.367	0.273	1.346	0.189
Home - Mixed Sterile inocula	26	0.015	0.273	0.055	0.956

Table 5- Summary table of planned comparisons from the linear mixed model of belowground productivity of mesocosm communities, where soil origin and soil content were fixed factors, and turf origin was the random factor.

Belowground biomass					
Contrast	<i>df</i>	Mean difference	SE	<i>t</i> -value	<i>P</i> -value
Home- Away Field soil	153	0.000	0.003	0.042	0.966
Home-Mixed Field soil	154	0.004	0.003	1.259	0.209
Home - Away Live inocula	160	0.001	0.004	0.390	0.696
Home - Mixed Live inocula	162	-0.059	0.004	-1.068	0.287
Home - Away Sterile inocula	24.2	-0.002	0.011	-0.243	0.810
Home - Mixed Sterile inocula	24.5	0.015	0.273	-1.562	0.131

Table 6- Summary table of planned comparisons from the linear mixed model of species richness of mesocosm communities, where soil origin and soil content were fixed factors, and turf origin was the random factor.

Community species richness					
Contrast	<i>df</i>	Mean difference	SE	<i>t</i> -value	<i>P</i> -value
Home- Away Field soil	165	-0.080	-0.331	-0.383	0.740
Home-Mixed Field soil	164	-0.140	-0.578	-0.152	0.564
Home - Away Live inocula	164	-0.464	-2.219	-0.314	0.027
Home - Mixed Live inocula	164	-0.268	-1.269	-0.395	0.206
Home - Away Sterile inocula	26	-0.286	-0.615	1.346	0.544
Home - Mixed Sterile inocula	26	0.571	1.229	0.055	0.230

Table 7- Summary table of planned comparisons from the linear mixed model of the evenness of mesocosm communities, where soil origin and soil content were fixed factors, and turf origin was the random factor.

Community evenness					
Contrast	<i>df</i>	Mean difference	SE	<i>t</i> -value	<i>P</i> -value
Home- Away Field soil	163	0.018	-0.331	0.725	0.469
Home-Mixed Field soil	163	0.007	-0.578	0.300	0.764
Home - Away Live inocula	161	-0.067	-2.219	-2.217	0.028
Home - Mixed Live inocula	159	-0.047	-1.269	-1.556	0.121
Home - Away Sterile inocula	26	0.020	-0.615	0.325	0.747
Home - Mixed Sterile inocula	26	-0.030	1.229	-0.494	0.625

Table 8- Relative species abundances across home soil mesocosm communities. The common species across all communities are indicated in boldface. Species present within communities as a result of seed rain are denoted by asterisks.

Species	Life strategy	Mean relative abundance in home soil communities
<i>Poa pratensis</i> L.	Perennial	0.556
<i>Bromus inermis</i> Leyss	Perennial	0.485
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex-Griffiths	Perennial	0.266
<i>Artemisia ludoviciana</i> Nutt.	Perennial	0.190
<i>Geum triflorum</i> Pursh.	Perennial	0.135
<i>Artemisia frigida</i> Willd.	Perennial	0.124
<i>Symphyotrichum falcatum</i> (Lindl.) G.L. Nesom	Perennial	0.100
<i>Drymocallis arguta</i> (Pursh) Rydb.	Perennial	0.097
<i>Rosa arkansana</i> Porter.	Perennial	0.094
<i>Symphyotrichum laeve</i> (L.) A. & D. Löve	Perennial	0.049
<i>Achillea millefolium</i> L.	Perennial	0.066
<i>Plantago major</i> L.	Perennial	0.056
<i>Festuca hallii</i> Vasey	Perennial	0.055
<i>Carex</i> sp.	Perennial	0.055
<i>Agrostis scabra</i> Willd.	Perennial	0.049
<i>Fallopia convolvulus</i> (L.) A. Love	Annual	0.048
<i>Elymus trachycaulus</i> (Link) Gould	Perennial	0.047
<i>Solidago missouriensis</i> Nutt.	Perennial	0.047
<i>Thermopsis rhombifolia</i> (Pursh) Richardson	Perennial	0.046
<i>Chenopodium album</i> L.	Annual	0.031
<i>Pascopyrum smithii</i> (Rydb.) A. Love	Perennial	0.026
<i>Lactuca tatarica</i> (L.) C.A. Mey.	Perennial	0.026
<i>Hesperostipa curtiseta</i> (A.S. Hitchc.) Barkworth	Perennial	0.022

<i>Sonchus arvensis</i> L.	Perennial	0.022
<i>Arabis hirsuta</i> L.	Perennial	0.021
<i>Gaillardia aristata</i> Pursh.	Perennial	0.018
<i>Poa sandbergii</i> J. Presl.	Perennial	0.017
<i>Taraxacum officinale</i> L.	Perennial	0.017
<i>Galium boreale</i> L.	Perennial	0.014
<i>Erigeron glabellus</i> Nutt.	Perennial	0.013
<i>Ulmus americana</i> L. *	Perennial	0.011
<i>Androsace septentrionalis</i> L.	Perennial	0.010
<i>Vicia americana</i> Muhl. ex Willd.	Perennial	0.009
<i>Cerastium arvensis</i> L.	Perennial	0.009
<i>Viola adunca</i> Sm.	Perennial	0.008
<i>Portulaca oleracea</i> L. *	Annual	0.008
<i>Thlaspi arvensis</i> L.	Annual	0.008
<i>Sagina procumbens</i> L. *	Perennial	0.007
<i>Oenothera sp.</i> *	N/A	0.006
<i>Gnaphalium uliginosum</i> L.*	Annual	0.006
<i>Crepis tectorum</i> L.	Annual	0.006
<i>Campanula rotundifolia</i> L.	Perennial	0.006
<i>Cirsium arvensis</i> (L.) Scop.	Perennial	0.005
<i>Astragalus dasyglottis</i> Dougl. ex G. Don	Perennial	0.003

Table 9- Summary table of the mean natural log transformed shoot biomass response ratios of the common species in the mesocosm experiment grown with field soils. Response ratios indicate species relative shoot productivity in soils conditioned by their own community and soil conditioned by a different community. *P*-values obtained following a one sample *t*-test.

Species	Mean	<i>t</i> -value	<i>df</i>	<i>P</i> -value
<i>Agrostis scabra</i>	0.160	0.245	12	0.810
<i>Artemisia ludoviciana</i>	-0.108	-0.345	34	0.731
<i>Bromus inermis</i>	0.369	1.438	4	0.223
<i>Carex sp.</i>	0.307	1.819	43	0.075
<i>Elymus trachycaulus</i>	0.312	0.593	10	0.566
<i>Festuca hallii</i>	-0.436	-0.957	6	0.375
<i>Poa pratensis</i>	-0.094	-0.737	74	0.462
<i>Symphotrichum laeve</i>	0.110	0.181	7	0.861

Table 10- Summary table of the mean natural log transformed shoot biomass response ratios of the common species in the mesocosm experiment grown with live inocula soil. Response ratios indicate species relative shoot productivity in soils conditioned by their own community and soil conditioned by a different community. *P*-values obtained following a one sample t-test.

Species	Mean	<i>t</i> -value	<i>df</i>	<i>P</i> -value
<i>Agrostis scabra</i>	-0.191	-0.543	9	0.599
<i>Artemisia ludoviciana</i>	0.142	0.448	24	0.657
<i>Bromus inermis</i>	0.647	2.640	5	0.045
<i>Carex sp.</i>	0.266	1.384	42	0.173
<i>Elymus trachycaulus</i>	-0.031	-0.068	13	0.964
<i>Festuca hallii</i>	0.117	0.201	4	0.850
<i>Poa pratensis</i>	0.044	0.420	75	0.675
<i>Symphotrichum laeve</i>	0.868	0.733	3	0.516

Table 11- Summary table of the mean natural log transformed shoot biomass response ratios of the common species in the mesocosm experiment grown with sterile inocula soils. Response ratios indicate species relative shoot productivity in soils conditioned by their own community and soil conditioned by a different community. *P*-values obtained following a one sample t-test.

Species	Mean	<i>t</i> -value	<i>df</i>	<i>P</i> -value
<i>Agrostis scabra</i>	0.625	0.652	3	0.560
<i>Artemisia ludoviciana</i>	0.191	0.400	9	0.697
<i>Bromus inermis</i>	1.794	0.980	1	0.506
<i>Carex sp.</i>	-0.633	-1.385	9	0.199
<i>Elymus trachycaulus</i>	0.422	0.443	2	0.701
<i>Festuca hallii</i>	-0.213	-0.527	2	0.650
<i>Poa pratensis</i>	0.005	0.023	11	0.981
<i>Symphyotrichum laeve</i>	0.090	0.165	2	0.883

Table 12- Linear regression summary table of relationship between the aboveground biomass log response ratio of mesocosm communities grown with field soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate aboveground net primary productivity of communities grown when grown on their own soils relative to when grown on soil from another community.

	Site field soil biomass log response ratio				Site field soil absolute biomass log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	0.0237	0.0798	0.297	0.768	0.1411	0.0449	3.138	0.0032
Site dissimilarity	0.1000	0.1682	-0.595	0.556	0.1934	0.0947	2.043	0.0480
Observations	40				40			
<i>r</i> ²	0.0092				0.0989			

Table 13 - Linear regression summary table of relationship between the species richness log response ratio of mesocosm communities grown with field soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate species richness of mesocosm communities when grown on their own soils relative to when grown on soil from another community.

	Site field soil species richness log response ratio				Site field soil absolute species richness log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	0.1269	0.0803	1.580	0.122	0.1885	0.0413	4.562	<0.001
Site dissimilarity	-0.0119	0.1807	-0.066	0.055	0.1405	0.0870	1.616	0.114
Observations	40				40			
<i>r</i> ²	0.0934				0.0642			

Table 14- Linear regression summary table of relationship between the species evenness log response ratio of mesocosm communities grown with field soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate species evenness of mesocosm communities when grown on their own soils relative to when grown on soil from another community.

	Site field soil species evenness log response ratio				Site field soil absolute species evenness log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	0.3027	0.1305	2.319	0.025	0.1411	0.0449	3.138	<0.001
Site dissimilarity	-0.5019	0.2748	-1.826	0.075	0.1934	0.0947	2.043	0.0048
Observations	40				40			
R2	0.0806				0.1907			

Table 15- Linear regression summary table of relationship between the aboveground biomass log response ratio mesocosm communities grown with live inocula soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate aboveground net primary productivity of communities grown when grown on their own soils relative to when grown on soil from another community.

	Site live inocula soil biomass log response ratio				Site live inocula soil absolute biomass log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	-0.0131	0.0848	-0.155	0.878	0.2600	0.0470	5.529	<0.001
Site dissimilarity	-0.0119	0.1807	-0.066	0.947	-0.0465	0.1001	-0.464	0.644
Observations	42				42			
R2	0.0001				0.0053			

Table 16- Linear regression summary table of relationship between the species richness log response ratio of mesocosm communities grown with live inocula soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate species richness of mesocosm communities when grown on their own soils relative to when grown on soil from another community.

	Site live inocula soil species richness log response ratio				Site live inocula soil absolute species richness log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	-0.1023	0.0920	-1.112	0.273	0.2978	0.0614	4.844	<0.001
Site dissimilarity	0.0634	0.1960	0.324	0.748	-0.1351	0.1309	-1.032	0.308
Observations	42				42			
R2	0.0026				0.0259			

Table 17- Linear regression summary table of relationship between the species evenness log response ratio of mesocosm communities grown with live inocula soils and the compositional dissimilarity between the turf communities the soils originate from. Log response ratios indicate species evenness of mesocosm communities when grown on their own soils relative to when grown on soil from another community.

	Site live inocula soil species evenness log response ratio				Site live inocula soil absolute species evenness log response ratio			
	Estimate	SE	<i>t</i>	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	-0.1336	0.1333	-1.002	0.322	0.4370	0.0952	4.590	<0.001
Site dissimilarity	-0.0519	0.2838	-0.183	0.856	-0.2205	0.2027	-1.088	0.283
Observations	42				42			
<i>r</i> ²	0.0008				0.0287			

Figures

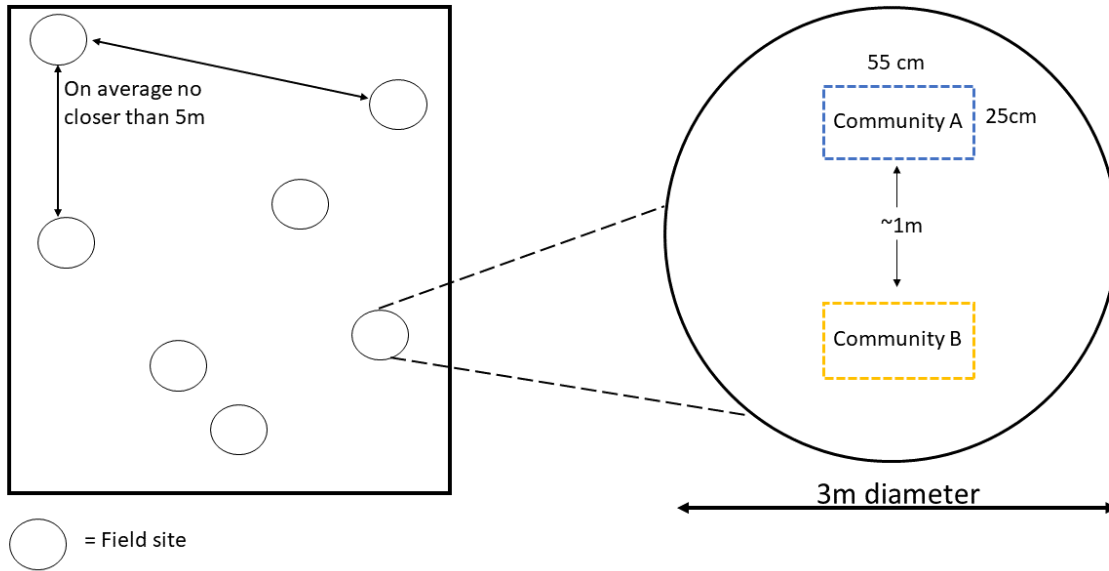


Figure 1 - Sampling protocol of the 42 sites within the Roy Berg Kinsella Research Ranch, located in Alberta, Canada. At each site a 3m diameter area was delineated, two 55x25cm quadrats were established ensuring they were separate by approximately 1m. From these quadrats, turf communities were extracted as well as the soils that were used to establish the mesocosm communities.

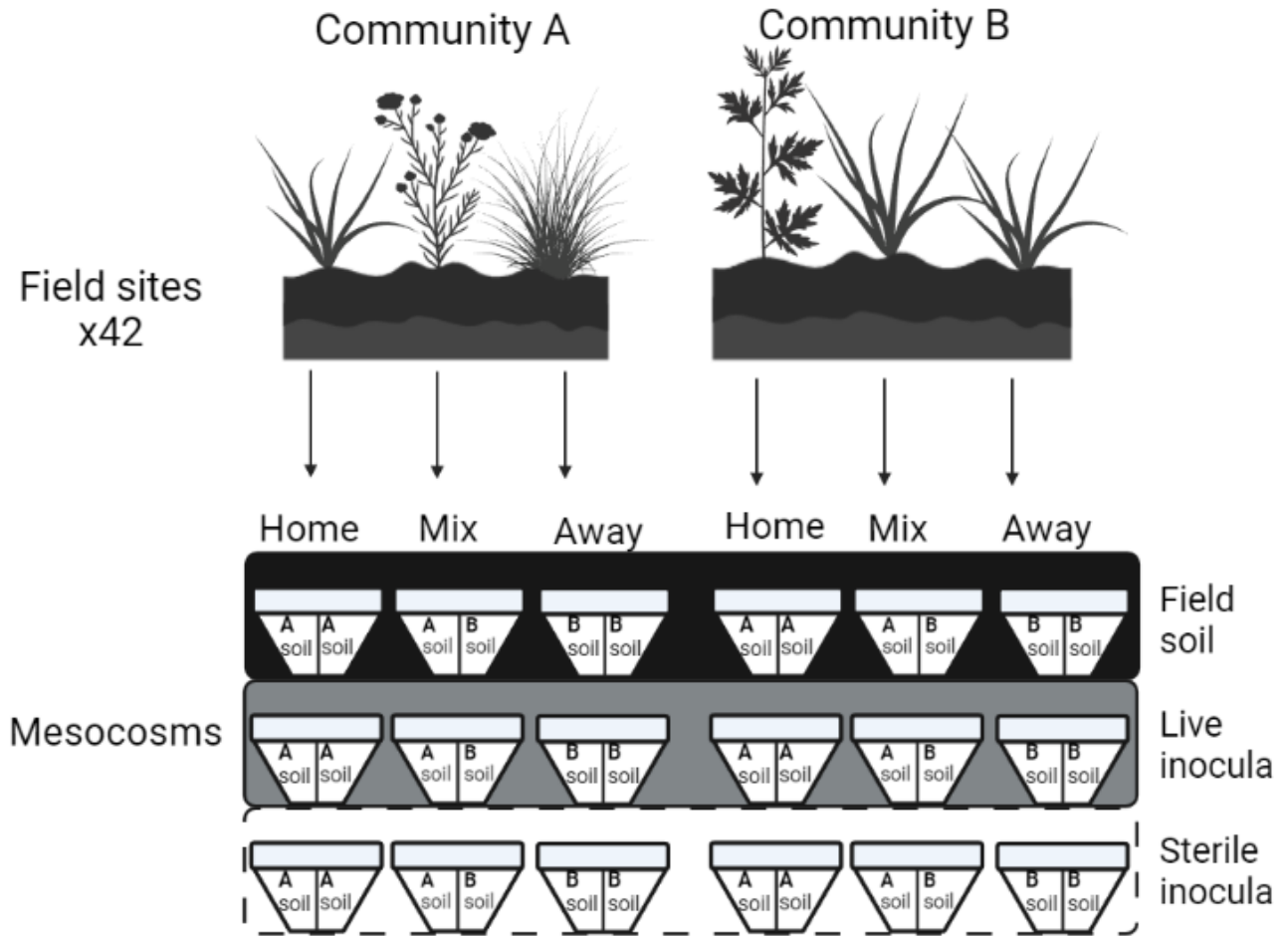


Figure 2- Overview of the mesocosm experiment. Pairs of turf communities were collected at 42 different sites within the study area. For each pair, a turf segment from each community was transplanted into a pot filled with soil collected from its own turf (home), from the other turf within the pair (away), or from both turfs (mix). The pots were filled either with field soils or field soil used as an inoculum. For 7 pairs, turf segments were also grown in a sterilized version of the inocula soils.

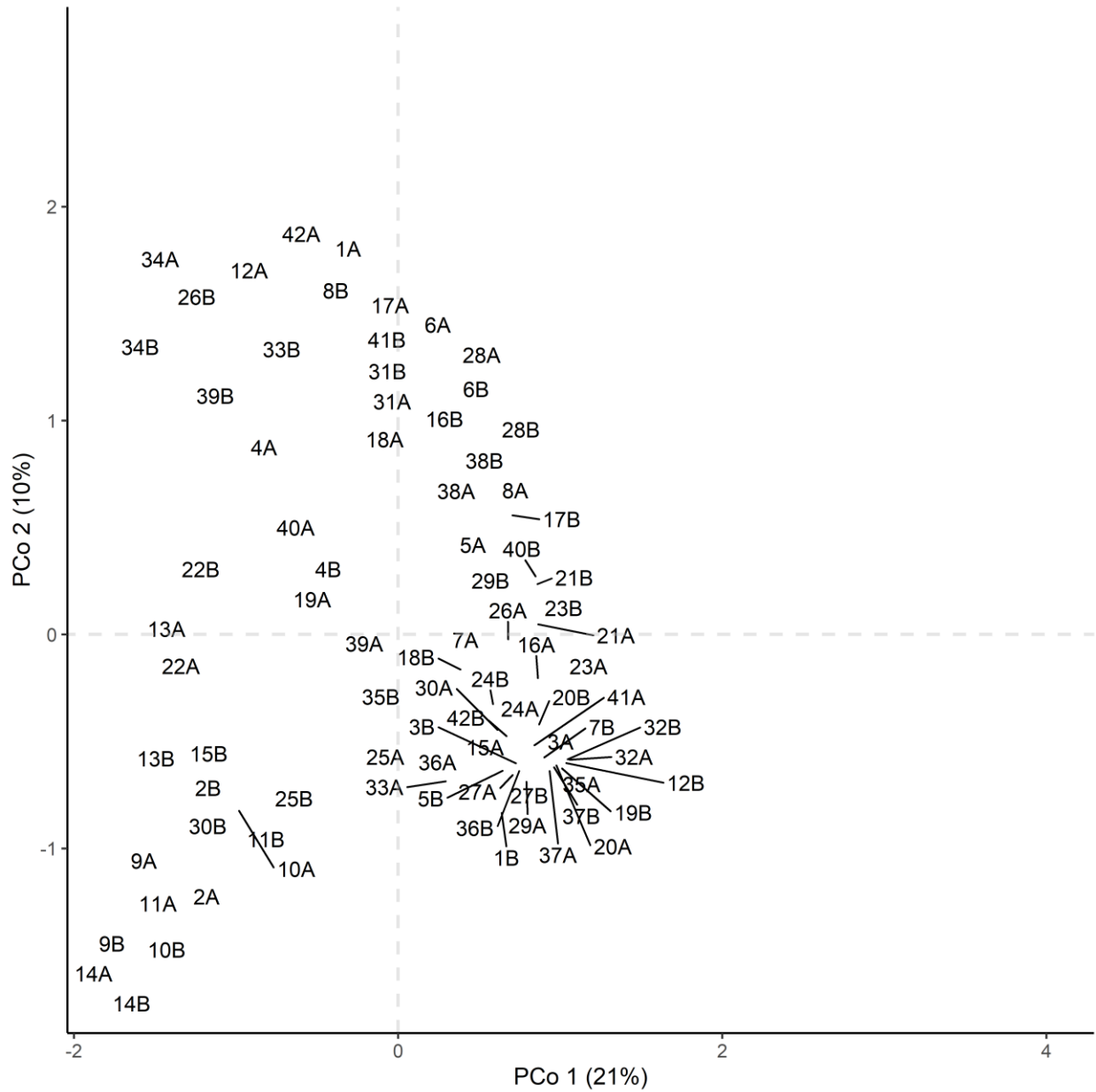


Figure 3- PCoA ordination of turf communities based on the Bray-Curtis dissimilarity of species composition. Numbers indicate the site of origin for each turf, as listed in Table 1. Letters distinguish individual turf communities within pairs collected at each site. The assignment of turfs as ‘A’ or ‘B’ was random. Percent variation explained by each principal coordinate axis is given within brackets.

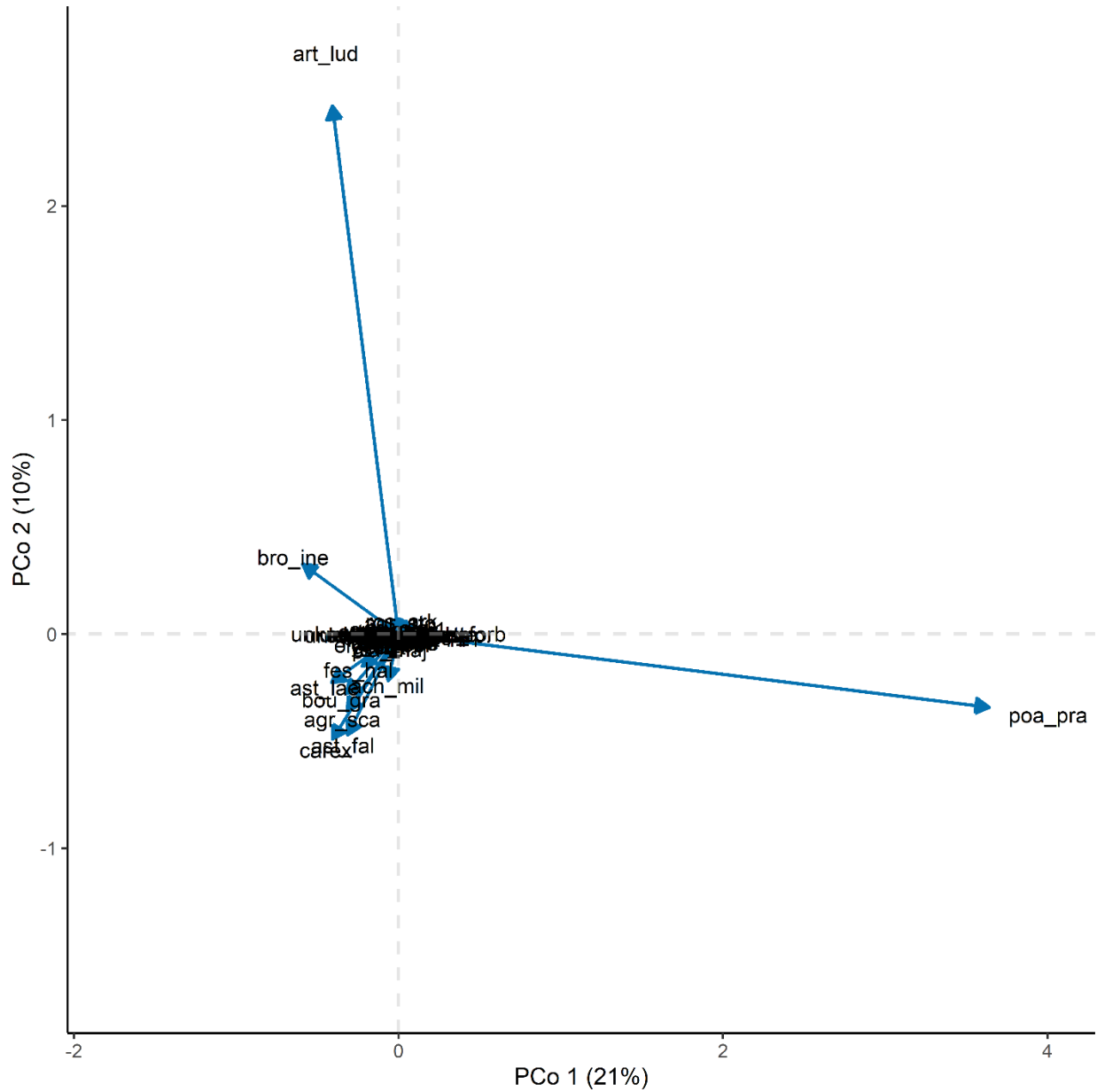


Figure 4- Species scores of the PCoA ordination of turf communities based on Bray-Curtis dissimilarity of species composition. Species scores are shown separately here to help visualize ordination. Percent variation explained by each principal coordinate axis is given within brackets.

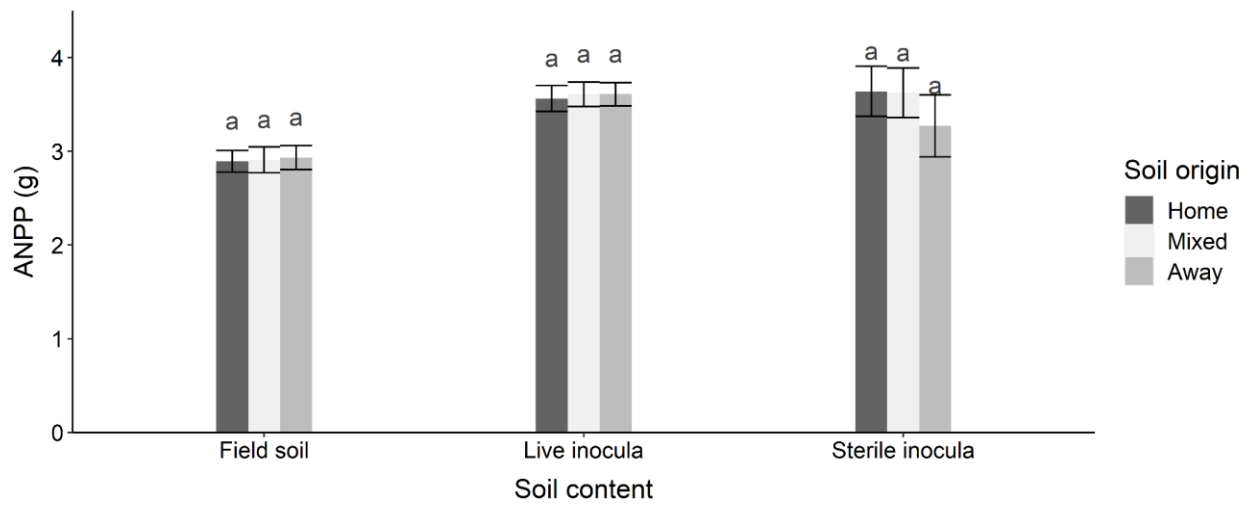


Figure 5- Mean aboveground net primary productivity of mesocosm communities based on soil content and origin. Communities grew with field soils or with field soils as inocula that were unsterilized (live) or sterilized. Error bars represent +/-SE. Different letters above bars indicate significant differences at $p < 0.05$ following planned comparisons between home soil and the two other soil origins within each soil content treatment.

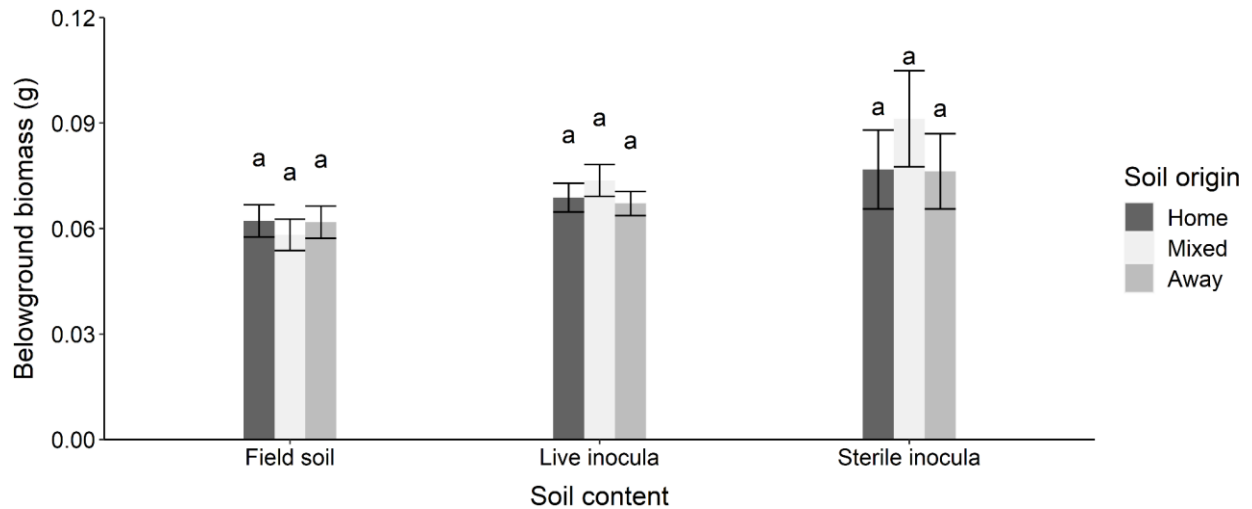


Figure 6- Mean belowground biomass of mesocosm communities based on soil content and origin. Communities grew with field soils or with field soils as inocula that were either left unsterilized (live) or sterilized. Error bars represent +/-SE. Different letters above bars indicate significant differences at $p < 0.05$ following planned comparisons between home soil and the two other soil origins within each soil content treatment.

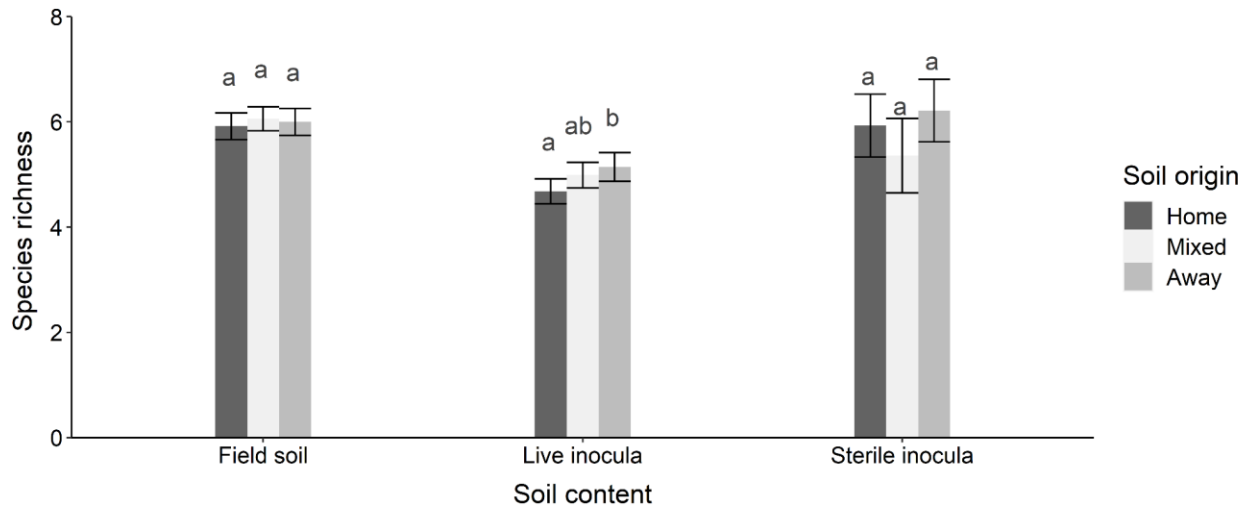


Figure 7- Mean species richness of mesocosm communities based on soil content and origin. Communities grew with field soils or with field soils as inocula that were either left unsterilized (live) or sterilized. Error bars represent +/-SE. Different letters above bars indicate significant differences at $p < 0.05$ following planned comparisons between home soil and the two other soil origins within each soil content treatment.

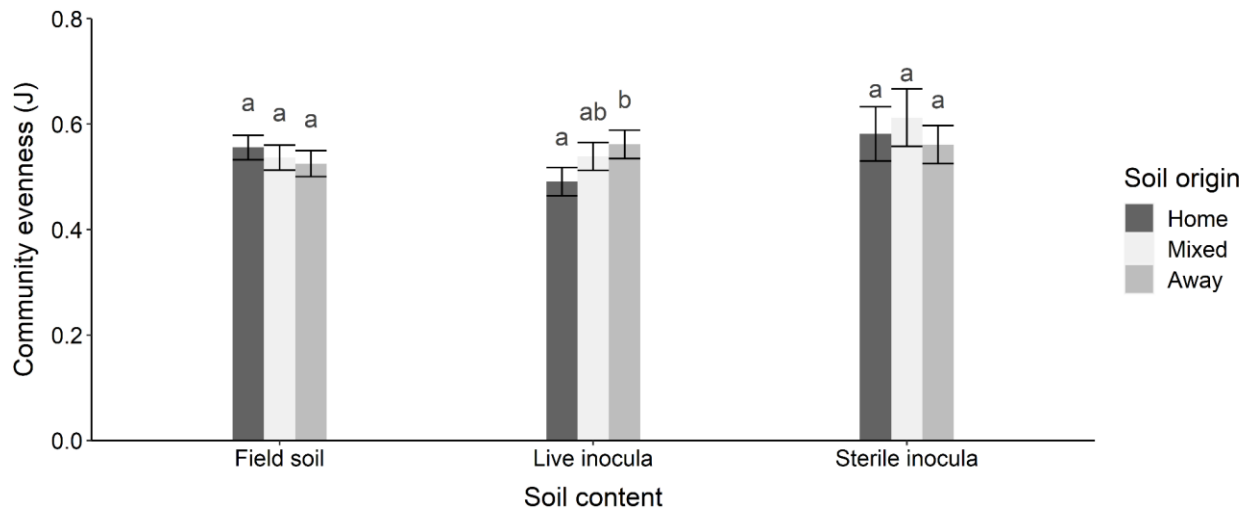


Figure 8- Mean evenness of mesocosm communities based on soil content and origin. Communities grew with field soils or with field soils as inocula that were either left unsterilized (live) or sterilized. Error bars represent +/-SE. Different letters above bars indicate significant differences at $p < 0.05$ following planned comparisons between home and the two other soil origins within each soil content.

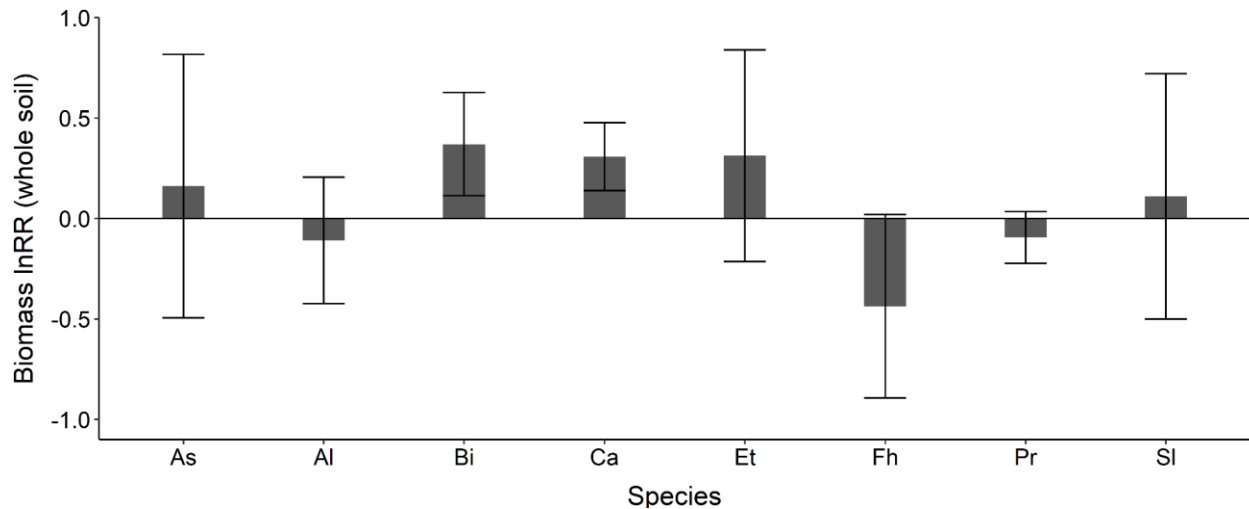


Figure 9- Mean natural log response ratios of aboveground biomass production for common species within mesocosm communities grown with field soils. Error bars represent \pm SE. Response ratios indicate species shoot productivity in soils conditioned by their own home communities relative to productivity in soils conditioned by a different community. Positive values denote a relative increase of shoot growth in home soil conditions, negative values denote a relative decrease of shoot growth in home soil conditions. No response ratio was statistically significant different from zero. As= *Agrostis scabra*, Al= *Artemisia ludoviciana*, Bi= *Bromus inermis*, Ca= *Carex sp.*, Et= *Elymus trachycaulus*, Fh= *Festuca hallii*, Pr= *Poa pratensis*, Sl= *Symphotrichum laeve*.

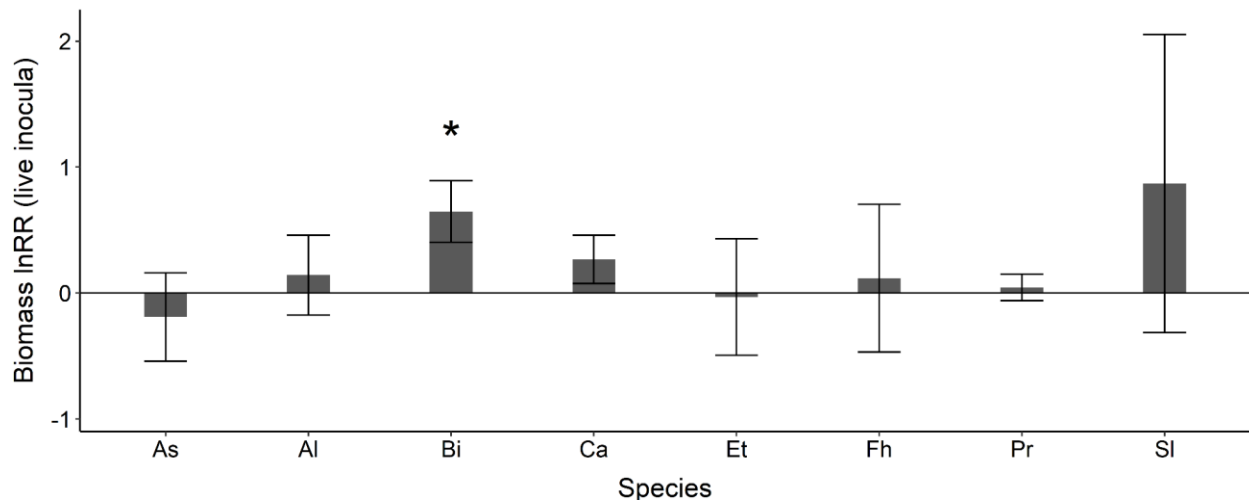


Figure 10- Mean natural log response ratios of aboveground biomass production common species within mesocosm communities grown with live inocula soils. Error bars represent \pm SE. Response ratios indicate species shoot productivity in soils conditioned by their own home communities relative to productivity in soils conditioned by a different community. Positive values denote relative increase of shoot growth in home soil conditions, negative values denote a relative decrease of shoot growth in home soil conditions. Asterisk above the bar indicates response ratios that significantly deviate from zero. As= *Agrostis scabra*, Al= *Artemisia ludoviciana*, Bi= *Bromus inermis*, Ca= *Carex sp.*, Et= *Elymus trachycaulus*, Fh= *Festuca hallii*, Pr= *Poa pratensis*, Sl= *Symphotrichum laeve*.

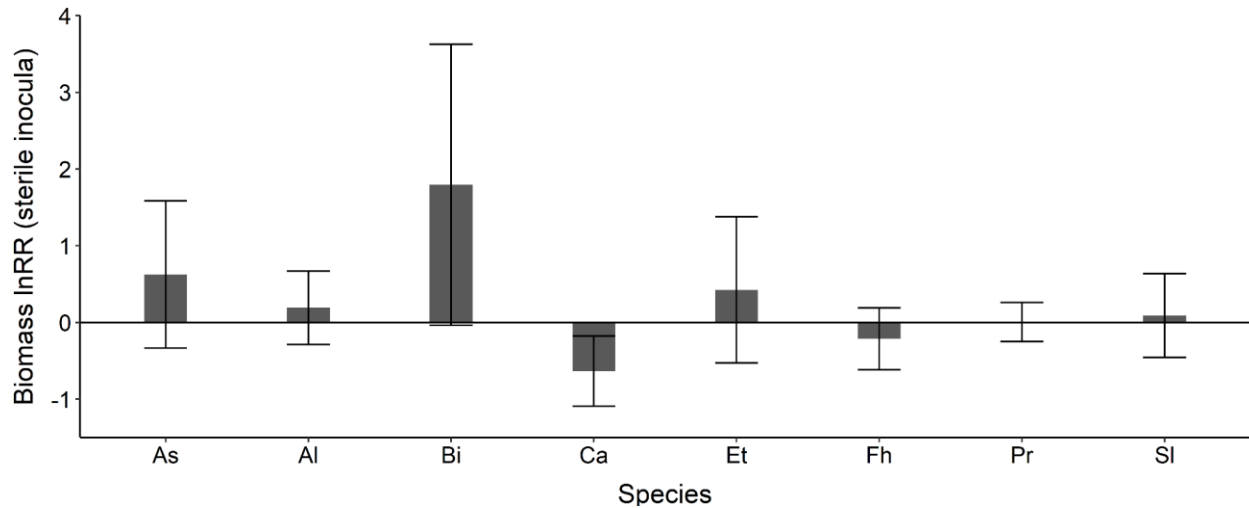


Figure 11- Mean natural log response ratios of aboveground biomass production for common species within mesocosm communities grown with sterilized inocula soils. Error bars represent \pm SE. Response ratios indicate species shoot productivity in soils conditioned by their own home communities relative to productivity in soils conditioned by a different community. Positive values denote a relative increase of shoot growth in home soil conditions, negative values denote a relative decrease of shoot growth in home soil conditions. No response ratio was statistically significant different from zero. As= *Agrostis scabra*, Al= *Artemisia ludoviciana*, Bi= *Bromus inermis*, Ca= *Carex sp.*, Et= *Elymus trachycaulus*, Fh= *Festuca hallii*, Pr= *Poa pratensis*, Sl= *Symphyotrichum laeve*.

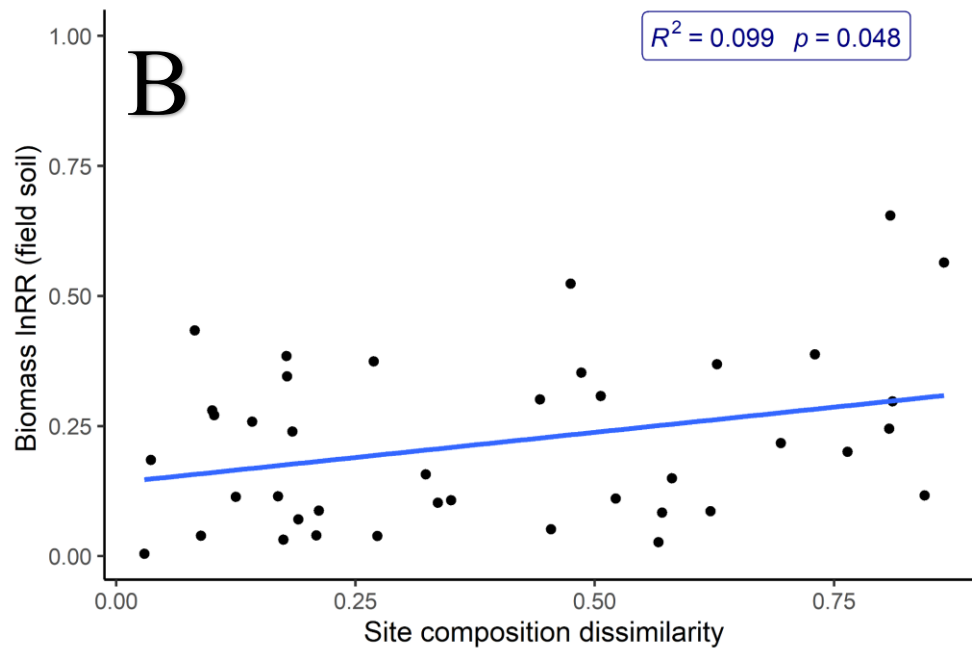
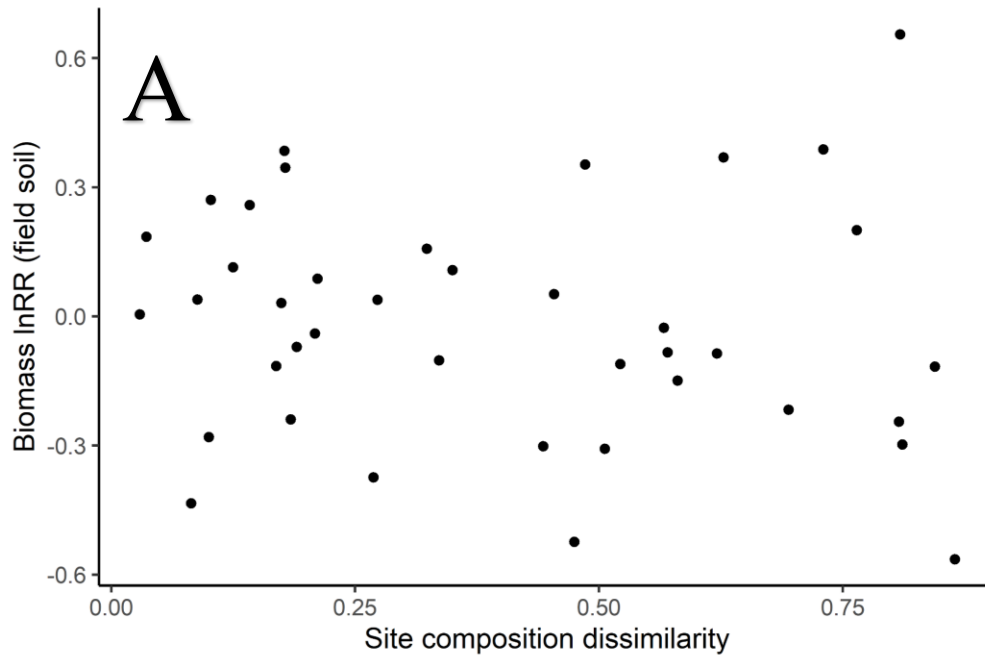


Figure 12- The relationship between the compositional dissimilarity of community origin of soils at a site and the natural log-transformed biomass response ratios of mesocosm communities in home and away field soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community productivity and negative values indicating reduced community productivity in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

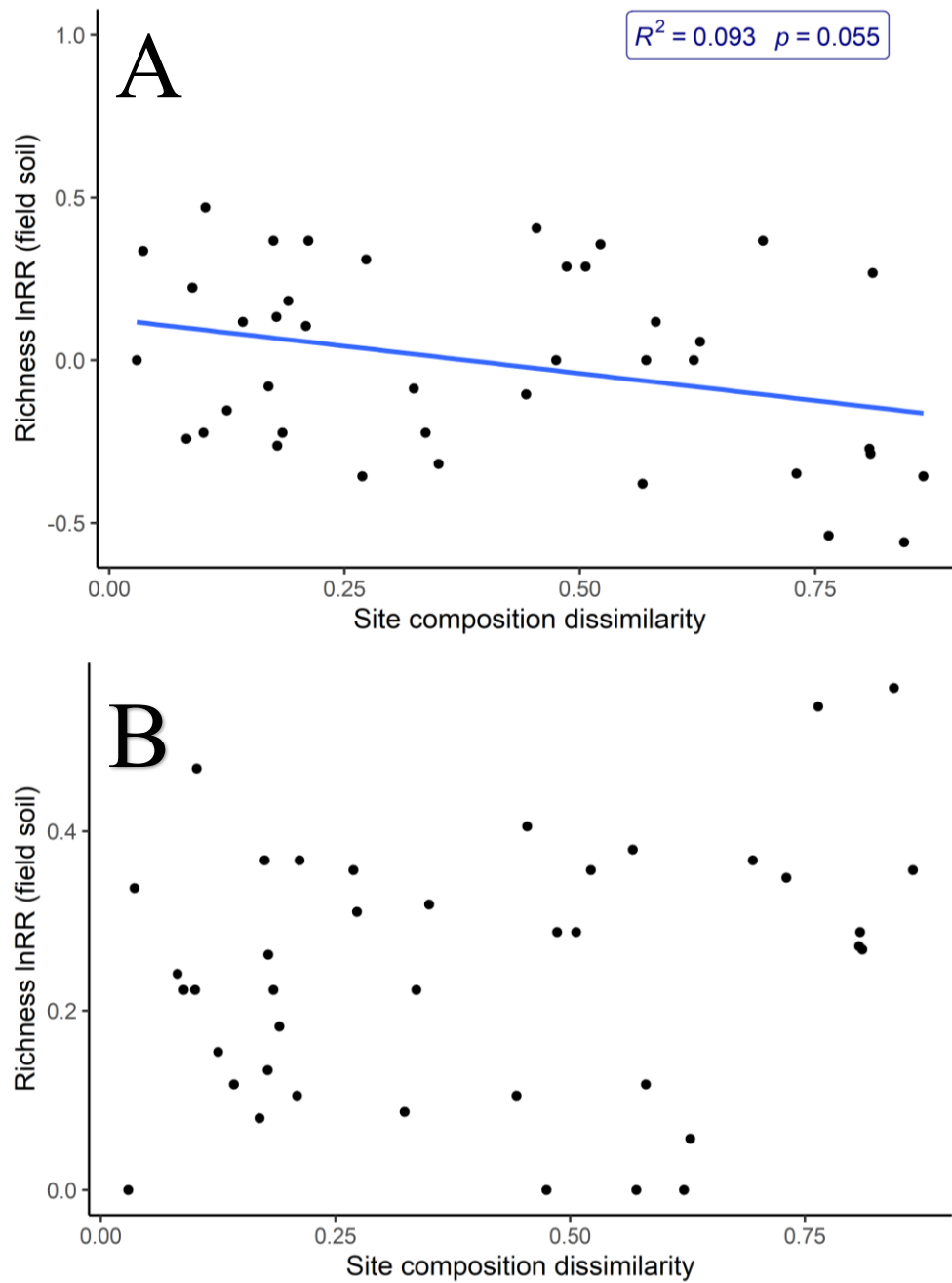


Figure 13- The relationship between compositional dissimilarity of community origin of soils at a site and the natural log-transformed species richness response ratios of mesocosm communities in home and away field soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community species richness and negative values indicating reduced community species richness in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

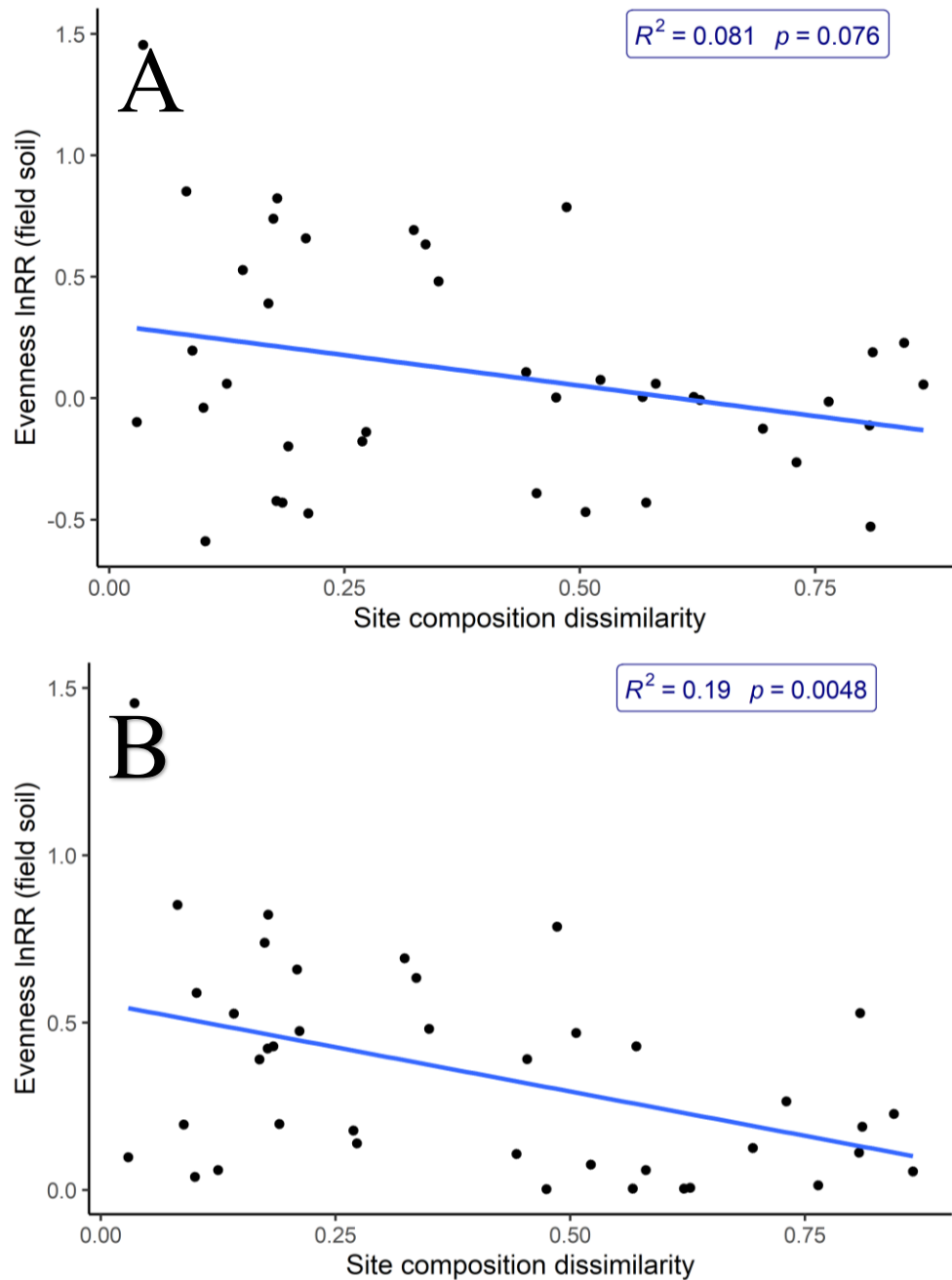


Figure 14- The relationship between compositional dissimilarity of community origin of soils at a site and the natural log-transformed species evenness response ratios of mesocosm communities in home and away field soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community species richness and negative values indicating reduced community species richness in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

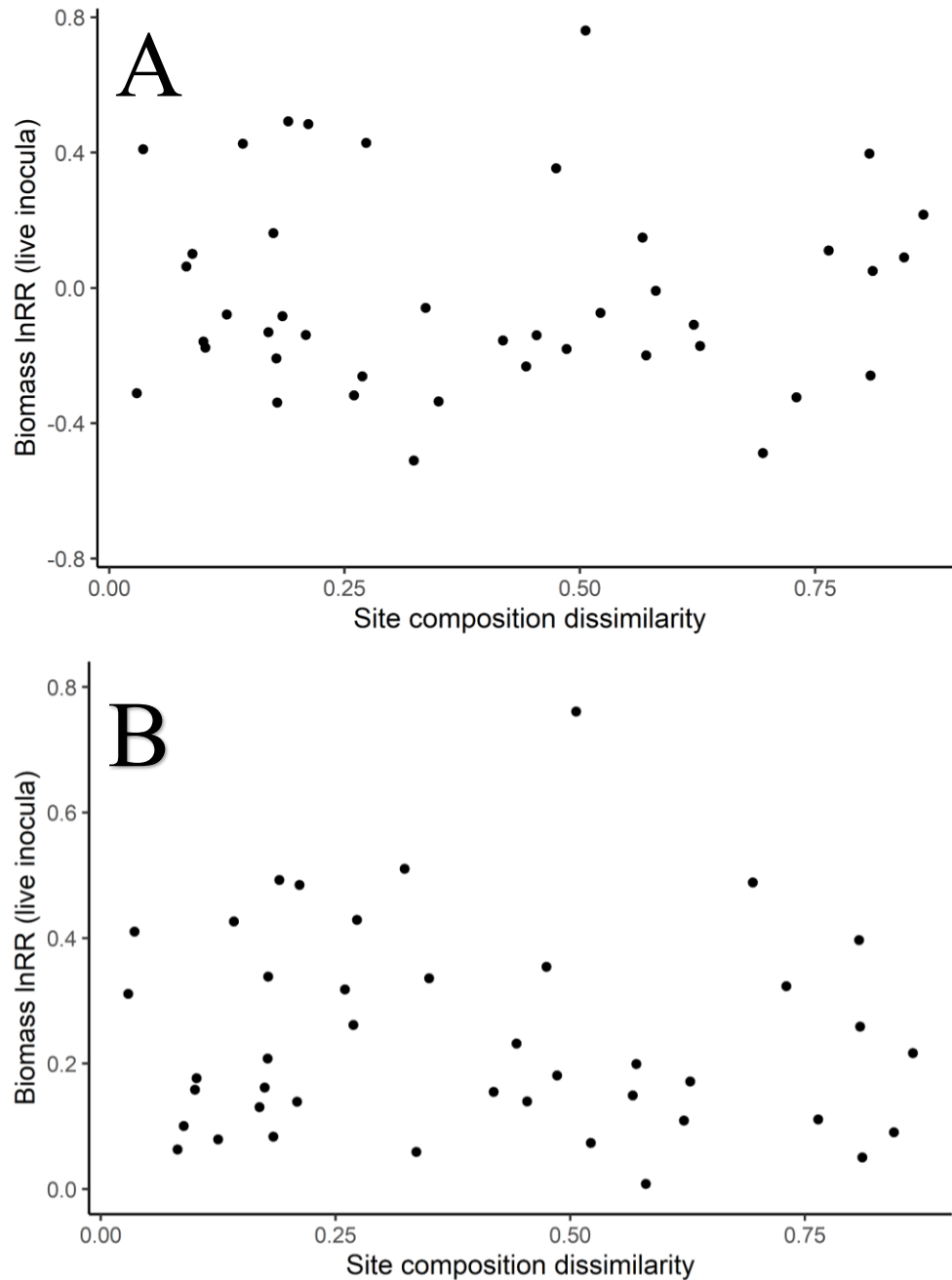


Figure 15- The relationship between the compositional dissimilarity of community origin of soils at a site and the natural log-transformed biomass response ratios of mesocosm communities in home and away live inocula soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community productivity and negative values indicating reduced community productivity in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

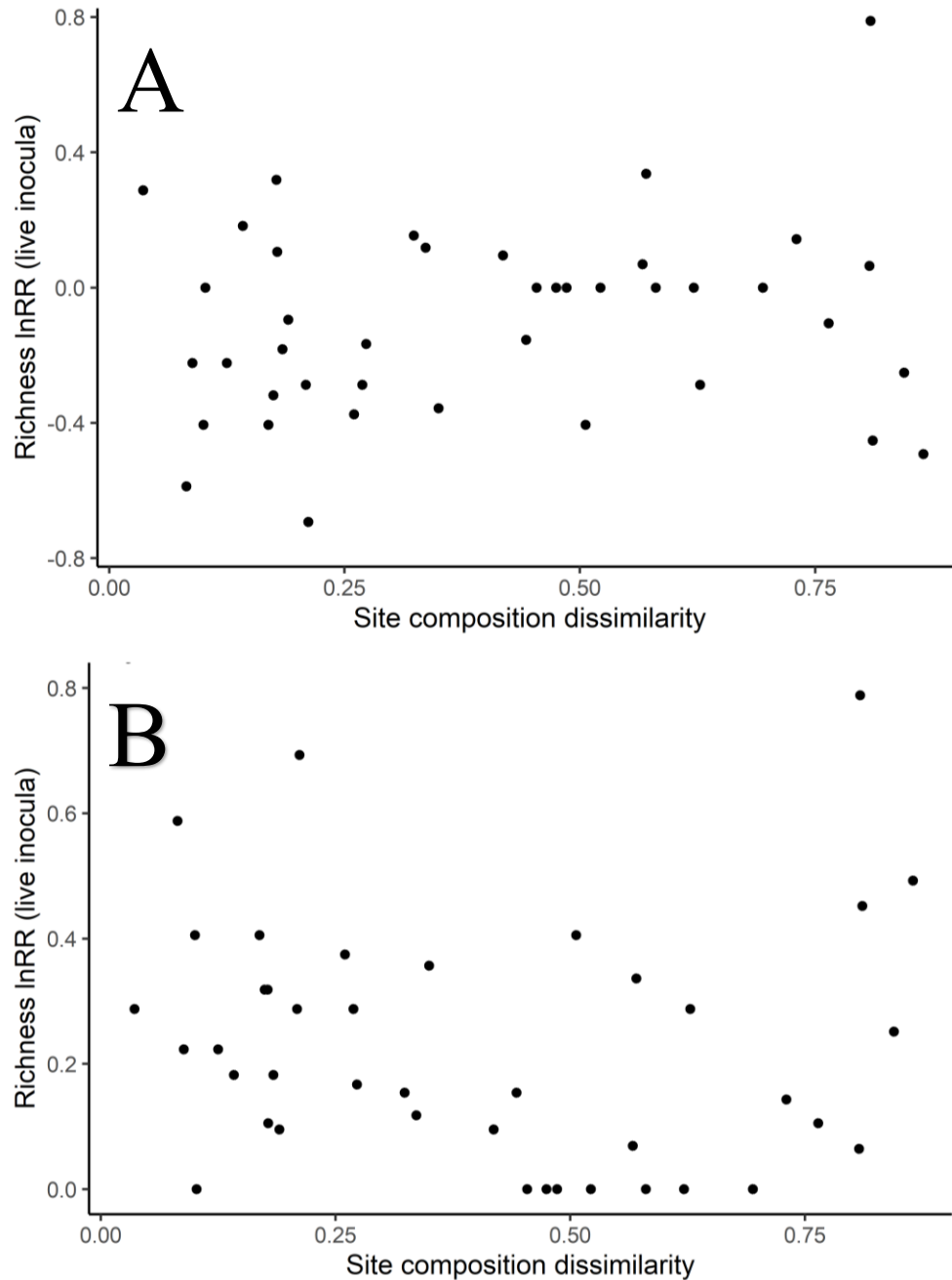


Figure 16- The relationship between compositional dissimilarity of community origin of soils at a site and the natural log-transformed species richness response ratios of mesocosm communities in home and away live inocula soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community species richness and negative values indicating reduced community species richness in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

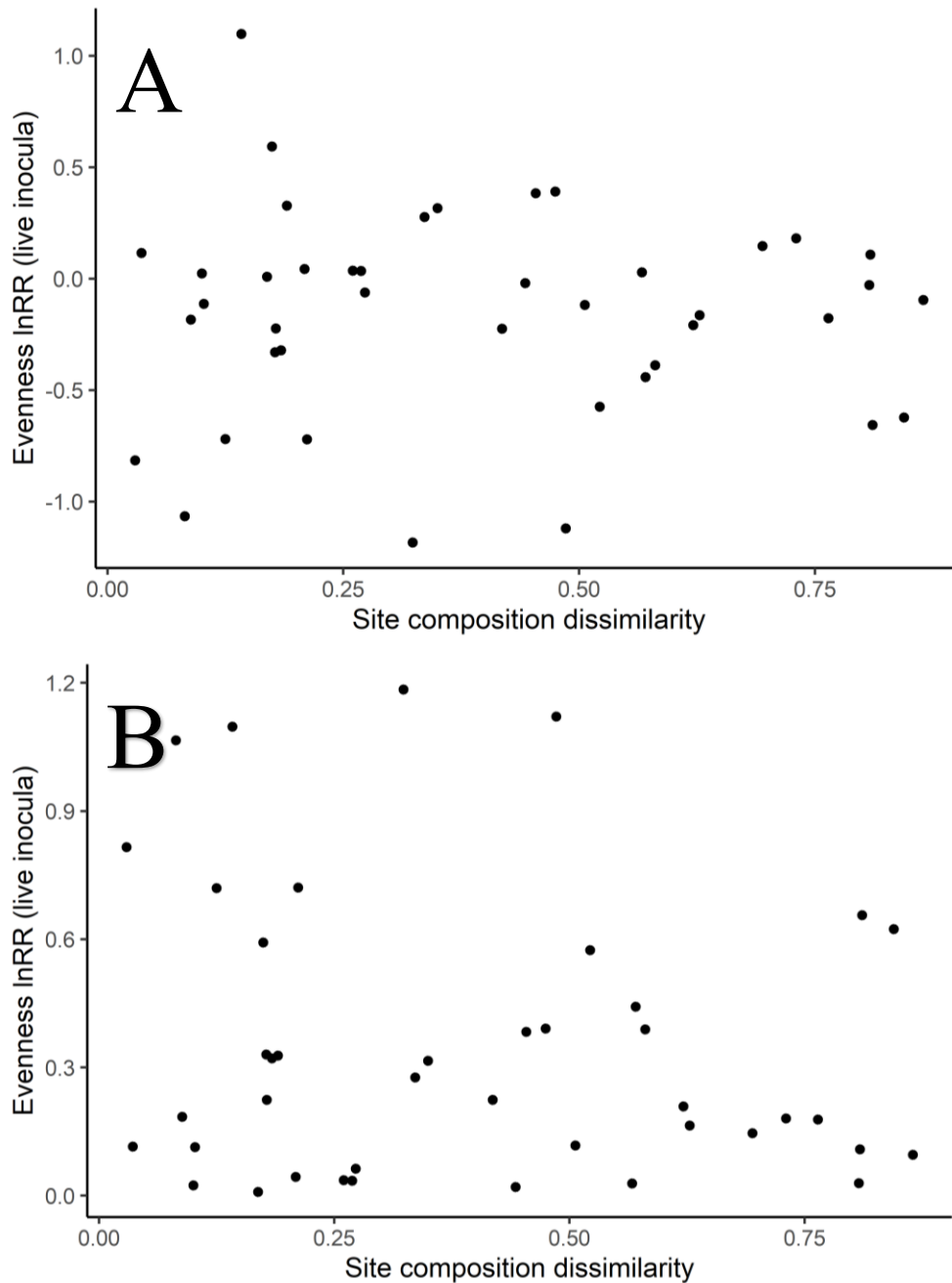


Figure 17- The relationship between compositional dissimilarity of community origin of soils at a site and the natural log-transformed species evenness response ratios of mesocosm communities in home and away live inocula soils. Panel (a) illustrates the directional relationship of response ratios with positive values indicating greater community species richness and negative values indicating reduced community species richness in home soil relative to away soils. Panel (b) showcases the relationship with absolute values of the response ratios.

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