Temporal dynamics of plant-soil feedbacks and community consequences during *Bromus inermis* invasion

by

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ABSTRACT

Invasive plant species often come to dominate the community where they have become introduced, posing a serious threat to plant diversity and ecosystem functions. Yet, the long-term dynamics and impacts of invasive species do not necessarily remain constant and may attenuate over time due to stabilizing mechanisms of plant-soil feedbacks. In this study, I first explored temporal dynamics of plant-soil feedbacks for the invader *Bromus inermis* (Leyss.) to determine whether invasive species accumulate negative plant-soil feedbacks over time. To fully capture all of the variations in plant-soil feedbacks for *B. inermis*, I used the combined strategy pairing field study with controlled conditions of the greenhouse environment to estimate *B. inermis* dynamics in natural systems while separating the potential drivers of plant-soil feedbacks. I found that *B. inermis* experience weakly negative to neutral plant-soil feedbacks in the early stages of invasion, but develops strongly negative plant-soil feedbacks over time. Contrary to our expectations, these shifts in the strength and directions of plant-soil feedbacks for *B. inermis* were not fully mediated by soil microbial communities of invaded areas. Second, I tested for environmental context dependence of plant-soil feedbacks for *B. inermis* by estimating changes in resource availability of invaded areas in relation to *B. inermis* residence time. The resource availability of *B. inermis*-invaded areas was at least partially associated with temporal dynamics of plant-soil feedbacks, where the increase in phosphorus availability and lower light access resulted in stronger, more negative plant-soil feedbacks for *B. inermis*. Last, I evaluated whether accumulation of negative plant-soil feedbacks for *B. inermis* can facilitate resident species recovery in invaded areas and result in lower *B. inermis* performance and dominance over time. No decline in *B. inermis* performance has been observed. Instead, *B. inermis* increased in shoot biomass production and allocated towards more vegetative reproduction under the effect of stronger negative plant-soil feedbacks. I also found that accumulation of negative plant-soil feedbacks for *B. inermis* was positively associated with recovery of species diversity but other factors of invaded areas can overcome the effect of plant-soil feedbacks and further mediate negative impacts of *B. inermis* invasion. The responses observed in this study suggest that at least in Alberta, *B. inermis* may accumulate stronger negative plant-soil feedbacks over time while still being dominant within a community. Yet, environmental context dependence of these plant-soil feedbacks can help us to predict under which conditions invasive species tend to experience more negative plant-soil feedbacks, allowing us to take advantage of invasive forage species while preventing/reducing their impact on biodiversity.

PREFACE

This thesis is collaborative work between myself, Dr. James Cahill, Charlotte Brown, and Gisela Stotz at the University of Alberta. My responsibilities included method development, data collection and processing, statistical analysis and interpretation, and manuscript composition. Dr. James Cahill was involved in concept formation and manuscript composition. Charlotte Brown and Gisela Stotz were involved in data collection. All research presented in this thesis was conducted in accordance with all applicable laws and rules set forth by provincial and federal governments and the University of Alberta. All necessary training and permits were obtained prior to data collection.

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1. INTRODUCTION

Some invasive plant species are widely recognized as a major threat to native biodiversity and ecosystem stability (Ehrenfeld 2003; Vilà *et al.* 2011). They can displace resident species through increased competition (Vilà and Weiner 2004; Lankau *et al.* 2009; Dostál 2011), or the production of novel allelochemicals (Callaway *et al.* 2005). The dominance of invasive species in the new range is often explained by the alternation of the soil environment through nutrient addition (Levine *et al.* 2003; Ehrenfeld 2003; Lai *et al.* 2018) or a decrease in the abundance of soil organisms that are beneficial for neighboring species (Callaway *et al.* 2008).

The long-term dynamics and impacts of plant invasion do not necessarily remain constant (Strayer *et al.* 2006; Strayer 2012), and the stabilizing mechanisms of plant-soil feedbacks may decrease invasive species dominance within a community and facilitate resident species recovery (Bever 1994, 2003; Hawkes *et al.* 2007; Dostál *et al.* 2013). For example, invasive plant species generally modify soil properties to their own advantage, thus creating positive plant-soil feedbacks (Klironomos 2002; but see Stotz *et al.* 2018). The effects of positive plant-soil feedbacks may also result from leaving behind natural enemies that regulate invasive species populations in their native range (Colautti *et al.* 2004; Power and Mitchell 2004), and enhanced interactions with symbiotic mutualists of invaded area (Reinhart and Callaway 2006; Callaway *et al.* 2011; Gundale *et al.* 2014). Nevertheless, any such advantage exerted by invasive species in the new range may attenuate over time, shifting plant-soil feedbacks towards more negative, whereby invasive plants species reduce in growth in their own soil (Hawkes *et al.* 2007; Diez *et al.* 2010; Flory and Clay 2013; Dostál *et al.* 2013; but see Day *et al.* 2015). First, as invasive plant species expand in distribution, they have a higher probability to encounter co-occurring pathogens (Gilbert and Webb 2007) that may negatively impact their performance over time. Second, novel biotic interactions of invasive species with pathogens, herbivores, and mutualists may form through adaptive evolution (Maron *et al.* 2004; Carroll *et al.* 2005; Bossdorf *et al.* 2005; Prentis *et al.* 2008), ultimately affecting the long-term dynamics of plant invasion. To our knowledge, however, most of the studies that examined the effects of plant-soil feedbacks mediated by soil biotic interactions are either derived from natural systems where time since introduction is unknown (Diez *et al.* 2010; Dostál *et al.* 2013) or short-term greenhouse experiments (Bennett and Cahill 2016; Chagnon *et al.* 2018). Both methodological approaches have been critical to providing empirical support for the strong influence of soil biota on plant invasion over time; however, simplified systems are unlikely to capture all of the variations in temporal dynamics of plant-soil feedbacks (Smith - Ramesh *et al.* 2017). It should be the combined strategy pairing field study with controlled conditions of the greenhouse environment to fully capture species dynamics in natural systems while separating the potential drivers of plant-soil feedbacks (Smith - Ramesh *et al.* 2017; Chung *et al.* 2019).

In addition to linking temporal dynamics of plant-soil feedbacks with soil biota of invaded community, identifying how environmental factors alter the direction and strength of plant-soil feedbacks is essential for developing effective management strategies and predicting the impact of plant invasion. For example, if nutrient-rich soils typically harbor more detrimental organisms than low-nutrient soils (Thrall *et al.* 2007; Revillini *et al.* 2016; but see Chagnon *et al.* 2018), then increased nutrient availability by invasive species (Liao *et al.* 2008) could promote larger pathogen infection and thus more negative plant-soil feedbacks over time. The importance of mutualists in plant invasion may also decrease (Kiers *et al.* 2003; Jr 2010) if limiting resources are maximized and invasive species become less dependent upon nutritional benefits from associated microbes (Revillini *et al.* 2016; Smith - Ramesh *et al.* 2017). A similar pattern was shown for the effect of light availability where weaker, less negative plant-soil feedbacks are expected to accumulate under high light (Smith and Reynolds

2015) due to poorer conditions for pathogens and/or enhanced plant defense against soil enemies (Augspurger 1984; Augspurger and Kelly 1984; McCarthy-Neumann and Ibáñez 2013). Yet, the specific effects of light availability on the dynamics of plant-soil feedbacks in the context of invasion remains largely unknown with only a few studies to this date, producing conflicting results (McCarthy-Neumann and Ibáñez 2013; Smith and Reynolds 2015). A better understanding of the environmental context dependence of plant-soil feedbacks can help us identify conditions under which invasive plant species are more likely to accumulate negative plant-soil feedbacks over time that may result in the decrease of invasive species dominance within an invaded community (Smith - Ramesh *et al.* 2017).

If invasive plant species experience increased negative plant-soil feedbacks over time, this could have variable effects on resident plant community structure and dynamic (Kulmatiski *et al.* 2008; Smith - Ramesh *et al.* 2017). For example, invasive species promote the accumulation of pathogens over time, this could increase pathogen-driven biotic attacks on co-occurring species and further reduce their ability to compete against invasive species (Strayer 2012; Flory and Clay 2013). Alternatively, if negative plant-soil feedbacks for invasive species involve host-specific pathogens, this may promote coexistence and diversity of the resident community by preventing invasive juveniles from reoccupying sites after the death of adults (Janzen 1970; Connell 1971; Petermann *et al.* 2008). However, negative plant-soil feedbacks mediated by soil microbial communities of invaded areas may also have little to no effect on the long-term dynamics of plant invasion due to greater expression of tolerance of invasive species to infections and diseases (Inglese and Paul 2006), compensation effects (Alexander 2010), and/or phenotypic plasticity (Packer and Clay 2004; Mordecai 2011). For example, a study by Alexander and Mihail (2000) found that high seedling mortality due to pathogen infection in *Kummerowia stipulacea* did not translate into decreased reproductive output of plant populations, suggesting that disease on individual plants and on plant populations are not necessarily equivalent. There thus is a need to test for the effects of increased negative plant-soil feedbacks on population growth of invasive species in their invaded areas, as it may help us to predict the long-term dynamics and impacts of plant invasion in natural systems.

In this study, we evaluated whether temporal dynamics of plant-soil feedbacks for an invasive species, *Bromus inermis* Leyss, can facilitate resident species recovery in invaded areas and result in the decline of *B. inermis* performance and dominance over time. Key characteristics of *B. inermis* invasion are the greatly reduced species diversity (Bennett *et al.* 2014; Stotz *et al.* 2017; Mamet *et al.* 2017), the increased soil nutrient availability, and the modification of soil microbial communities (Piper *et al.* 2015a, b; Stotz *et al.* 2019). Past greenhouse work also revealed that *B. inermis* experience negative plant-soil feedbacks when grown in its own soil while resident species increase in tolerance to *B. inermis* in soil from invaded areas (Stotz *et al.* 2018), thus motivating the current study. First, we conducted a long-term experiment that tracked *B. inermis* invasion along 6-m transects and captured changes in community characteristics that became invaded within the time frame of this study. Then, utilizing soils collected from the field, we established a greenhouse experiment to answer the following questions:

1. Does *B. inermis* accumulate negative plant-soil feedbacks over time, and is it mediated through microbial communities of invaded areas? How does the effect of negative plant-soil feedbacks for *B. inermis* translate into the population growth of *B. inermis*?
2. How does time since introduction of *B. inermis* in invaded areas interact with resource availability to alter the strength and direction of plant-soil feedbacks? If resource availability affects the dynamics of plant-soil feedbacks for *B. inermis*, is it mediated through interactions with microbial communities of invaded areas?

3. What are the long-term impacts of *B. inermis* on plant community structure, and can negative plant-soil feedbacks for *B. inermis* facilitate the recovery of invaded areas over time?

2. METHODS

2.1. Study system

Bromus inermis Leyss. (smooth brome) is a perennial cool-season grass native to central Eurasia that was intentionally introduced to Canada as a forage crop in the late 1800s (Otfinowski *et al.* 2007). Following its introduction, *B. inermis* has escaped from cultivation and has since been ranked as one of the most harmful invasive species in Canada (Catling and Mitrow 2005). It may establish along different habitats, but its most detrimental impact seems to be on the diversity of prairies and native grasslands (Grace *et al.* 2001; Stacy *et al.* 2005; Otfinowski *et al.* 2007; Carrigy *et al.* 2016). Where it invades, *B. inermis* forms dense, large patches (~ 60% cover), significantly decreasing light availability and soil moisture (Fink and Wilson 2011; Bennett *et al.* 2014). *B. inermis* disperses through seeds and vegetative growth of tillers or rhizomes, facilitating its expansion into adjacent uninvaded areas (Otfinowski *et al.* 2007; Otfinowski and Kenkel 2008). *B. inermis* also tends to increases soil nutrient availability through litter accumulation and alters microbial communities (Piper *et al.* 2015a, b), which is thought to increase its invasive potential (Vinton and Goergen 2006; but see Carrigy *et al.* 2016).

To test for temporal dynamics of plan-soil feedbacks in the context of invasion, we focused on *B. inermis* invasion in the grasslands of Alberta, Canada (Otfinowski *et al.* 2007). The study took place at sites that vary in species richness and climatic conditions, ranging from a dry mixed grassland to the central aspen parkland ecoregion. Mattheis Research Ranch located within the dry mixed grassland has a mean annual precipitation of 246.79 mm and productivity of 703 g/m^2, and is dominated by grasses including *Hesperostipa comate* (needle-and-thread), *Koeleria macrantha* (junegrass), *Bouteloua gracilis* (blue grama), and *Calamovilfa longifolia* (sand grass). Roy Berg Kinsella Research Ranch located at the central aspen parkland ecoregion has a mean annual precipitation of 314.91 mm and productivity of 904.2 g/m^2, and is dominated by grasses including *Festuca hallii* (plains rough fescue), *Hesperostipa curtiseta* (western porcupine grass), and *Koeleria macrantha* (junegrass).

2.2. Sampling design

To quantify the long-term dynamics and impacts of *B. inermis* invasion we used a space-for-time substitution, where continuous encroachment of *B. inermis* into adjacent uninvaded areas along a small spatial scale (within 6-m transects; Figure 1a) served as a proxy for predicting residence time of *B. inermis* in their invaded areas. This method is commonly used in invasion studies (Vilà *et al.* 2006; Hejda and Pyšek 2006; Hejda *et al.* 2009; Powell *et al.* 2013; Kumschick *et al.* 2015) and is of great value for predicting the effects of invasive species over time (Strayer *et al.* 2006; Kumschick *et al.* 2015) when pre-invasion data are not available.

To determine the long-term dynamics and impacts of *B. inermis* invasion, 20 transects per site were set up in 2013 and have since been continuously monitored by the Cahill Lab of Experimental Plant Ecology. Each transect was 4 m long (extended to 6 m in 2015), running perpendicular to the edge of *B. inermis* patches, with 2 m into the invaded areas and the rest into native areas (for more details on transect design see Stotz *et al.* 2019). *B. inermis* presence was recorded at every 1 cm along each transect using a line-intercept method (Goldsmith and Sutherland 1997). The line-intercept method was specifically designed to quantify changes in cover and height over time and has been found to be an efficient method in grassland vegetation sampling (Mueller-Dombois and Ellenberg 1974; Caratti 2006). We then used a modified belt-transect method to measure gradual changes in community characteristics of *B. inermis* invaded areas (Grant *et al.* 2004). Within each transect we established ten 50 x 50 cm sampling plots ranging between invaded, recently invaded, and native areas (Figure 1b).

2.3. Measuring community structure and resource availability of B. inermis-invaded areas

At each sampling plot, we estimated light transmission by measuring photosynthetically active radiation (PAR) above and below the canopy with a linear PAR sensor (Decagon Devices Inc., Pullman, Washington, USA), and calculating it as the proportion of light above the canopy able to penetrate below the canopy. Measures were taken in July within ~2.5 h of solar noon on clear, sunny days. We then collected sieved soil samples to identify other abiotic properties under the laboratory conditions. Gravimetric moisture of each position was identified by weighing fresh and dried soil, and expressing it as the ratio of water to dry soil mass. Soil pH of each position was measured with a pH electrode in 10g soil mixed with 20 ml of Milli-Q water. Soil phosphorus was determined by extracting Mehlich-III available phosphorus from 2 g of soil using 20 ml of Mehlich-III reagent, followed by colorimetric analysis (Carter and Gregorich 2007).

To measure the dynamics and impacts of *B. inermis* invasion on community structure, we first identified species present within each sampling plot with an estimated cover. This provided us with a detailed characterization of invaded areas to calculate species richness and evenness. Species evenness of invaded community was estimated as $J = H0/\log(S)$, where H' is Shannon diversity index and S is total species richness. *B. inermis* was not included into the calculations (Thomsen *et al.* 2016). Second, we recorded number of *B. inermis* tillers in invaded areas to determine vegetative growth of *B. inermis* in response to temporal dynamics of plant-soil feedbacks. We also collected *B. inermis* biomass at the peak, separating it into litter, shoot, and flowering biomass. This allowed us to determine the population growth of *B. inermis* in natural systems, as well as reproductive effort of *B. inermis* in response to temporal dynamics of plant-soil feedbacks. Reproductive effort of *B. inermis* was calculated as *RE* = (*B. inermis* flowering biomass)/(*B. inermis* shoot biomass - *B. inermis* flowering biomass). Last, resident species biomass was collected, and all samples were dried at 70 °C for 48 hr and weighed.

2.4. Measuring temporal dynamics of plant-soil feedbacks for B. inermis *and mediation by microbial communities*

To determine the effects of residence time on the long-term dynamics of plant-soil feedbacks for *B. inermis*, we removed four 20-cm deep soil cores beneath the clipped vegetation from each sampling plot. Soils were sieved (4 mm diameter sieve) and packed separately to use as a living inoculum in a greenhouse experiment. Soils were stored at 4°C until the beginning of the greenhouse experiment, which was within 30 days of collection.

In order to investigate temporal dynamics of plant-soil feedbacks for *B. inermis* and the role of local soil microorganisms in mitigating those feedbacks, we set up a greenhouse experiment using two experimental approaches (Figure 2): whole-soil approach (large volumes of inoculum), as it allowed us to test for the total effect of soil properties on *B. inermis* performance, including nutrients and allelochemicals (Smith and Reynolds 2015), and an inoculum approach (small volumes of inoculum), as it allowed us to isolate the impact of soil biota (microbes and soil microfauna) on *B. inermis* performance while standardizing abiotic soil properties among replicates (Bever 1994; Brinkman *et al.* 2010).

To measure plant-soil feedbacks in the whole-soil approach, we grew *B. inermis* in soils from each sampling plot in 340-ml Styroblock pots (Beaver Plastics, Acheson AB, Canada) with a full addition of inoculum (full treatment). As a means of comparison, we also grew *B.*

inermis in potting soil that was not previously conditioned, vegetation-free (control treatment). The potting soil consisted of coarse sand, fine sand, and topsoil in a 2:1:1 ratio, and was autoclaved prior to the experiment at 121°C for 3 hr. For the inoculum approach, we grew *B. inermis* in pots containing a 9:1 mixture of potting soil and living inoculum (inoculum treatment) and compared to a similar mixture without soil community where living inoculum was autoclaved prior to the experiment at 121°C for 3 hr (no inoculum treatment). By evaluating changes in the strength and direction of plant-soil feedbacks between these two approaches, we were able to determine whether *B. inermis* can accumulate strong negative plant-soil feedbacks over time through interactions with soil microorganisms of invaded community, or through total effects of soil properties.

Plant seeds (purchased from Gold Medal Seeds, Brooks, AB Canada) were sown directly in 340-ml Styroblock pots and thinned to one individual per pot after 14 days (similar to Chagnon *et al.* 2018). Pots were arranged into 3 replicate blocks with one sampling plot for each soil treatment containing inoculum per block, which resulted in a total of 1350 pots (136 sampling plots x 3 treatments with inoculum x 3 replicates + 12 controls per block). *B. inermis* were left unfertilized, and watered as needed, during the course of the experiment. After 15 weeks, *B. inermis* shoot and root biomass were harvested to measure the growth. Roots were washed free of soil under tap water (1 mm diameter sieve), and then shoot and root biomass was dried at 70 °C for 48 hr and weighed.

2.5. *Quantifying the strength and direction of plant-soil feedbacks*

To quantify the strength and direction of plant-soil feedbacks for *B. inermis* in the whole-soil approach, we used the “own vs. foreign” feedback metric (Petermann *et al.* 2008; Brinkman *et al.* 2010), as it reflects total soil effects on *B. inermis* biomass when growing in its own soil, relative to the soil of different origin. The feedback response for each sampling plot was calculated as ln[biomass (full treatment)/ biomass(control treatment)]. The log-transformation was used to achieve normality and homogeneity of variances. At the same time, the log transformation returns zero when there is a neutral plant-soil feedback, or no difference in *B. inermis* biomass when grown in own soil versus foreign soil, a feedback response less than zero represents a negative plant-soil feedback, or *B. inermis* biomass reduction when grown in own soil versus foreign soil, and a feedback response greater than zero represents a positive plant-soil feedback, or an increased *B. inermis* biomass when grown in own soil versus foreign soil.

To quantify the strength and direction of plant-soil feedbacks for *B. inermis* in the inoculum approach, we used the "+ biota vs – biota" feedback metric (Petermann *et al.* 2008; Brinkman *et al.* 2010), as it reflects the cost of gain in *B. inermis* biomass when growing in its own soil with the addition of soil biota, relative to soil with no soil biota. The feedback response for each sampling plot was calculated as ln[biomass (inoculum treatment)/ biomass(no inoculum treatment)]. The log-transformation was used to achieve normality and homogeneity of variances. We get zero when there is no difference in *B. inermis* biomass when grown with soil biota versus no soil biota, indicating that soil microorganisms have no impact on *B. inermis* performance in invaded areas. A value greater than zero indicates that soil microorganisms of *B. inermis*-invaded areas increase *B. inermis* performance, while a value less than zero indicate that soil microorganisms of *B. inermis*-invaded areas reduce *B. inermis* performance.

2.6. The effect of temporal dynamics of plant-soil feedbacks for B. inermis and mediation by microbial communities

Using the long-term data on *B. inermis* abundance (Stotz *et al.* 2019), we first determined the rate of *B. inermis* expansion along the transects and evaluated the results with Akaike's Information Criterion (AIC) (Table 1). In this study, we examined linear

($y_i=\beta_0+\beta_1X_i+e_i$), quadratic ($y_i=\beta_0+\beta_1X_i+\ \beta_2X_i^2+e_i$), and logarithmic ($y_i=\beta_0+\beta_1\ln(X_i)+e_i$) models to capture temporal dynamics of *B. inermis* invasion that could be explained by interaction with microbial communities of invaded areas (Dickie *et al.* 2017). The dependent variable was y (time since introduction), the independent variable was *B. inermis* abundance along the transect measured since 2013, β_0 and β_2 were the coefficients to be determined, and e_i is random error. The best-fitted models were used to estimate how long each sampling plot within each transect has been invaded by *B. inermis* (time since introduction). In some cases, the introduction pathways and timing were less clear due to transects being fully invaded and/or disturbance, which results in the exclusion of 6 transects from the further analysis. This resulted in a total of 13 transects, with 2 transects extended to 7 m and 8 m (n=136).

To test for temporal dynamics of plant-soil feedbacks for *B. inermis* and the role of soil microorganisms in driving these feedbacks, we run linear mixed models using feedback response in the whole-soil approach and feedback response in the inoculum approach as response variables. Models were fit using the lmer function in the lme4 package in R [Bates *et al.* 2020]) with time since introduction as the explanatory variable. For each model, transect within site and block were used as random effects. Data were tested for normality and heteroscedasticity using visual techniques and the Shapiro-Wilks test.

Last, to access how the effects of plant-soil feedbacks for *B. inermis* translate into the population growth of *B. inermis*, we run linear mixed models with *B. inermis* shoot and litter biomass, number of *B. inermis* tillers, and reproductive effort in *B. inermis* as response variables. Models were fit using the lmer function in the lme4 package in R [Bates *et al.* 2020]) with the whole-soil approach plant-soil feedbacks as the explanatory variable and transect within site as a random effect. Data were tested for normality and heteroscedasticity using visual techniques and the Shapiro-Wilks test. Reproductive effort in *B. inermis* and number of *B. inermis* tillers were cube-root transformed due to negatively skewed distribution.

2.7. The effect of time since introduction on resource availability and alternation of plant-soil feedbacks for B. inermis

We first evaluated whether time since introduction caused changes in resource availability at the transect level. We run linear mixed models with soil moisture, light availability, pH, and soil phosphorus (P) as response variables. Models were fit using the lmer function in the lme4 package in R [Bates *et al.* 2020]) with time since introduction as the explanatory variable and site as a random effect. Data were tested for normality and heteroscedasticity using visual techniques and the Shapiro-Wilks test. Light transmission was cube-root transformed due to negatively skewed distribution, and pH was square-root transformed due to positively skewed distribution.

We then run linear mixed models to test for the interaction of plant-soil feedback for *B. inermis* with resource availability of invaded areas. The response variables, feedback response in the whole-soil approach and feedback response in the inoculum approach, were assessed with four separate models with explanatory variables of soil moisture, light availability, pH, and soil phosphorus (P) to test for their potential to mediate the accumulation of negative plant-soil feedbacks for *B. inermis*. For each model, site and block were used as random effects. Models were fit using the lmer function in the lme4 package in R [Bates *et al.* 2020]). Data were tested for normality and heteroscedasticity using visual techniques and the Shapiro-Wilks test. In both the whole-soil approach and the inoculum approach analysis, light transmission was cube-root transformed due to negatively skewed distribution, and pH was square-root transformed due to positively skewed distribution.

2.8. The effect of temporal dynamics of plant-soil feedbacks for B. inermis on community structure of invaded areas

To examine how community structure change in relation to temporal dynamics of plant-soil feedbacks for *B. inermis*, we used structural equation modeling (SEM) (Grace 2006; Lamb *et al.* 2011). This allows us to test the hypothesis that accumulation of negative plant-soil feedbacks for *B. inermis* may mediate the recovery of resident species diversity. Our first step was to develop an initial path model based on prior theoretical knowledge about species dynamics in the system (Figure 3; Stotz *et al.* 2019). In this study, we tested for the ability of negative plant-soil feedbacks for *B. inermis* to mediate changes in plant community structure over time, both directly or through changes in *B. inermis* shoot and litter biomass. As a measure of the change in community structure, we used species richness, evenness, and non-brome biomass. We normalized our data using min-max scaling to bring the variables to the same range. Mean values for all variables used in the models are given in Table 2. The second step was to evaluate the fit between the model and the actual structure of the data, as this will provide us with support for the theoretical relationships being tested. Models were fit using the lavaan library in R (Rosseel 2012) and evaluated based on criteria of chi-square, RMSEA, CFI, SRMR, and AIC values (Kline 2010). The best models did not achieve adequate fit as measured by the RMSEA values (<0.08), indicating a poor fit between models and data (Table 3). Yet, Kline (2010) discussed that these cut-off values should not necessarily be treated as absolutes, but the reasons for large RMSEA values need to be examined. Here, the issues with model fitting could be partly explained by the relatively small sample size (n=136), which could lead to errors in the estimation of covariances and thus a discrepancy between model-implied and observed covariances. Alternatively, the cut-off rules could become overly conservative when sample sizes are below 250 (Hu and Bentler 1999) thus creating uncertainties in the model fit.

Taken collectedly, the results of this structural equation modeling should be viewed as working hypotheses with a degree of empirical support.

3. RESULTS

3.1. The effect of temporal dynamics of plant-soil feedbacks for B. inermis and mediation by microbial communities

Time since introduction had a significant effect on the strength and direction of plant-soil feedbacks for *B. inermis* in the whole-soil approach ($F_{1,303} = 29.75$, $P < 0.0001$). Soils that were conditioned for longer harbored stronger and more negative plant-soil feedbacks, whereas soils from newly established *B. inermis* areas were associated with more neutral plant-soil feedbacks (Table 4, Figure 4a). Contrary to our expectations, we did not find evidence that accumulation of negative plant-soil feedbacks for *B. inermis* over time was mediated by soil microorganisms of invaded areas ($F_{1,300} = 0.51$, $P = 0.47$; Figure 4b), as indicated in the inoculum approach.

Consistent with the results above, we found no evidence that accumulation of negative plant-soil feedbacks for *B. inermis* translates into reduced population growth of *B. inermis* in natural systems (Table 5). In contrast, stronger negative plant-soil feedbacks were associated with increase of *B. inermis* shoot biomass ($F_{1,137} = 22.05$, $P = <0.0001$), but not with litter biomass production ($F_{1,296} = 1.06$, $P = 0.31$). Stronger negative plant-soil feedbacks were also associated with allocations towards more vegetative growth in *B. inermis* (Figure 5), as indicated by an increase in number of tillers ($F_{1,297} = 12.78$, $P = <0.01$) and decrease in reproductive effort during *B. inermis* invasion ($F_{1,134} = 3.98$, $P = 0.05$).

3.2. The effect of time since introduction on resource availability and alternation of plant-soil feedbacks for B. inermis

The effect of time since introduction on resource availability of invaded areas partially altered the strength and direction of plant-soil feedbacks for *B. inermis* in the whole-soil approach (Table 6-7, Figure 6-7). Light availability significantly changed in relation to time since introduction ($F_{1,90}$ =7.21, P < 0.01), and was associated with accumulation of negative plant-soil feedbacks for *B. inermis* under low light conditions ($F_{1,61}$ = 3.67, P < 0.05). Conversely, soil moisture did not change significantly in relation to time since introduction ($F_{1,90}$ = 0.12, P = 0.72), and it was also not associated with the dynamics of plant-soil feedbacks for B. *inermis* ($F_{1,16}$ = 1.15, P = 0.29). Consistent with results above, we found no change in pH in relation to time since introduction ($F_{1,89}$ = 1.67, P = 0.19) and no association with the dynamics of plant-soil feedbacks for *B. inermis* ($F_{1,36}$ = 2.61, P = 0.11). We found strong increase in phosphorus availability in relation to time since introduction ($F_{1,88}$ = 23.51, P <0.01). Increase in phosphorus availability resulted in significantly stronger negative plant-soil feedbacks for *B. inermis* ($F_{1,31}$= 4.81, P = 0.03). In the inoculum approach, the dynamics of plant-soil feedbacks for *B. inermis* were not dependent upon resource availability of invaded areas (Table 8).

3.3. The effect of temporal dynamics of plant-soil feedbacks for B. inermis on community structure of invaded areas

Time since introduction of *B. inermis* in invaded areas had a significant direct negative effect on plant species richness (b[direct]=-0.007, P<0.01). Yet, the accumulation of negative plant-soil feedbacks for *B. inermis* over time was found to slow down the impact of residence time (b[indirect]= 0.001, P<0.05) on invaded communities but not through reduction of *B. inermis* shoot biomass or *B. inermis* litter biomass (Table 9, Figure 8a). Instead, *B. inermis* litter biomass acted as the indirect effect of time since introduction on species richness and mediated the negative impact (b[indirect]= -0.004, P<0.01). The indirect mediation via *B. inermis* shoot biomass was found to be insignificant (b[indirect]= -0.001, P=0.08). This indicates that even if the accumulation of negative plant-soil feedbacks for *B. inermis* may reduce the impact of *B. inermis* invasion over time, the effect might not be strong enough as the total impact of time since introduction on species richness was found to be negative (b[total]= -0.011, P<0.01) indicating competitive partial mediation.

In contrast to the results above, plant species evenness of invaded areas was found to be not associated with the direct effect of time since introduction (b[direct]=-0.003, P=0.33; Table 10). Total impact of time since introduction was also found be insignificant (b[total]= -0.003, P=0.3) indicating no effect (no mediation). Yet, if we separate the specific indirect effects per mediator variable, we found that accumulation of negative plant-soil feedbacks for *B. inermis* could facilitate greater evenness of invaded areas (b=-0.13, P<0.01; Figure 8b) over time (b[indirect]= 0.001, P<0.05). On the other hand, the indirect effects via *B. inermis* litter biomass production mediated negative impact of time since introduction (b[indirect]= -0.001, P<0.05) on species evenness, indicating competitive mediation with the indirect effect of plant-soil feedbacks for *B. inermis*. The indirect mediation via just *B. inermis* shoot biomass was to found be insignificant (b[indirect]= -0.000, P=0.22).

Last, time since introduction of *B. inermis* in invaded areas had a significant direct negative effect on non-brome shoot biomass production (b[direct]=-0.022, P<0.01). Similar to the results above, accumulation of negative plant-soil feedbacks for *B. inermis* over time was found to slow down the impact of residence time (b[indirect]= 0.002, P=0.01) on invaded communities but not through reduction of *B. inermis* shoot biomass or *B. inermis* litter biomass (Table 11, Figure 8c). The indirect pathway of *B. inermis* litter biomass mediating the effect of time since introduction on non-brome biomass was found to be insignificant (b[indirect]=

0.000, P=0.45), as well as the indirect mediation via *B. inermis* shoot biomass (b[indirect]= -0.001, P=0.07). Total impact of time since introduction was found to be significantly negative (b[total]= -0.021, P<0.01), indicating competitive partial mediation and suggesting that some other variables of the invaded community may play a crucial role in mediating negative impacts of *B. inermis* invasion on non-brome shoot biomass production.

4. DISCUSSION

In this study, we searched for temporal dynamics of plant-soil feedbacks for *B. inermis* and mediation by soil microbial communities of invaded areas, environmental context dependence of plant-soil feedbacks, and a consequent change in *B. inermis* impact on plant community structure. Overall, *B. inermis* accumulated stronger negative plant-soil feedbacks in relation to residence time (Figure 4a); yet, we did not find evidence for the role of soil microorganisms driving these shifts in the long-term dynamics of *B. inermis* invasion (Figure 4b). We found that the strength and direction of plant-soil feedbacks for *B. inermis* were at least partially dependent upon environmental factors of invaded communities (Figure 7) with contrasting effects in the whole-soil approach versus the inoculum approach (Table 8). More importantly, we found that stronger, more negative plant-soil feedbacks for *B. inermis* could facilitate the recovery of resident species diversity (Figure 8), yet other factors of invaded communities may overcome the effect of plant-soil feedbacks. This information can provide insight into temporal dynamics of plant-soil feedbacks in the context of invasion and improve our ability to predict the outcomes of plant invasions.

4.1. The effect of temporal dynamics of plant-soil feedbacks for B. inermis and mediation by microbial communities

The reduced growth in soils that had been invaded longer by *B. inermis* (Figure 4a) demonstrates that over the course of the invasion, *B. inermis* alters local soil conditions in a way that negatively affects their subsequent growth. This pattern is broadly consistent with other studies on overtime accumulation of negative plant-soil feedbacks in the context of invasion (Diez *et al.* 2010; Flory and Clay 2013; Putten *et al.* 2013; Dostál *et al.* 2013; but see also Day *et al.* 2015). More specifically, our results supported findings that invasive plant species that became established longer ago exhibit stronger negative plant-soil feedbacks relative to weakly negative or neutral plant-soil feedbacks of newly established invaded sites (Diez *et al.* 2010), but found no evidence of positive plant-soil feedbacks, often seen for introduced species in the new range (Klironomos 2002; Reinhart *et al.* 2003; Callaway *et al.* 2004). The predominance of negative plant-soil feedbacks for *B. inermis* in invaded areas could be linked to *B. inermis* being a grass species (Kulmatiski *et al.* 2008) characterized by high root to soil contact which could increase grass exposure to belowground enemies. Interestingly, overall negative plant-soil feedbacks for *B. inermis* may help to explain why *B. inermis* invasion is successful in our systems. If *B. inermis* experience strong negative plant-soil feedbacks in the home range it is most likely to realize the benefits of enemy release in the new range (Kulmatiski *et al.* 2008). Then, *B. inermis* is most likely to invade and dominate grassland communities where negative plant-soil feedbacks for native grasses are common (Callaway *et al.* 2004; Putten *et al.* 2013; Smith-Ramesh and Reynolds 2015). Future research explaining the dynamics of plant-soil feedbacks for *B. inermis* in the home range and *B. inermis*-invaded grassland communities could reveal fundamental information to support these predictions and provide a screening tool for other potentially invasive grass species: species with strong negative plant-soil feedbacks in the home range may most likely become invasive in the new range. In this study, we know that even if *B. inermis* encounters weakly negative or neutral plant-soil feedbacks in the early stages of invasion, which may still facilitate its dominance in invaded communities (Callaway *et al.* 2004; Putten *et al.* 2013; Smith-Ramesh and Reynolds 2015) such initial advantage attenuate over time and stronger negative plant-soil feedbacks develop.

We found no support for the hypothesized microbial mediation that may shift plant-soil feedbacks for *B. inermis* towards more negative in soils that had been invaded longer (Flory and Clay 2013). The absence of negative soil-biotic plant-soil feedbacks in relation to residence time (Figure 4b) might be due to pathogen accumulation and the time required for their effect to manifest in individuals or populations (Hawkes *et al.* 2007; Mitchell *et al.* 2010; Day *et al.* 2015). For example, data from Hawkes (2007) suggest that 200 years may be required for pathogen attack, and *B. inermis* was first recorded in Alberta around the 1930s (Otfinowski *et al.* 2007). Similarly, stronger negative plant-soil feedbacks for *B. inermis* over time could be due to the accumulation of non-pathogenic soil microorganisms competing with roots for mineral nutrients, especially nitrogen (Liu *et al.* 2016) which could explain the difference between the whole-soil approach and the inoculum approach. Invasion by *B. inermis* has specifically been found to increase total soil nitrogen through litter input, likely prompting higher microbial activity and higher gross rates of nitrogen mineralization in invaded soils (Piper, *et al.* 2015a, b). If the increase in minimalization stimulates higher rates of microbial immobilization, plant-available nitrogen for *B. inermis* may be limited (Knops *et al.* 2002) which could potentially create stronger negative plant-soil feedbacks, but neither the intensity of this relation nor temporal dynamics of it are known. Last, we cannot exclude the possibility that the development of negative plant-soil feedbacks for *B. inermis* over time could be due to factors other than interaction with detrimental soil microorganisms of the invaded community (Smith - Ramesh *et al.* 2017). Nutrient availability tends to be greater in *B. inermis*-invaded areas, especially in relation to residence time (Figure 7; (Piper *et al.* 2015a, b; Stotz *et al.* 2019), which could result in *B. inermis* being less dependent upon nutritional benefits from associated microbes (Adesemoye *et al.* 2009; Leff *et al.* 2015; in ’t Zandt *et al.* 2019, and many more) and drive negative plant-soil feedbacks in nutrient-rich soils. However, temporal dynamics of such decreased mutualistic associations between invasive plant species and soil organisms of invaded communities remains to be demonstrated.

Although *B. inermis* accumulated negative plant-soil feedbacks over time, no decline in *B. inermis* abundance has yet been observed (Figure 5; Sinkins and Otfinowski 2012 but see Myhr *et al.* 1966; Waller 1979 for decline when in cultivation). This pattern is likely due to *B. inermis* being a forage species that has been selected for its fast and high-density growth under different conditions (Cook 1943; Wilkins and Humphreys 2003). Moreover, the competitive ability of *B. inermis* increases in high nutrient soils (Gendron and Wilson 2007; Holub *et al.* 2012; Carrigy *et al.* 2016) which could also explain *B. inermis* potential to develop strong negative plant-soil feedbacks while continuing to invade the community. However, the greater competitive ability of *B. inermis* in invaded areas is unlikely to be the sole mechanism explaining why negative plant-soil feedbacks for *B. inermis* did not translate into the population decline of *B. inermis* in natural systems. Previous greenhouse study found that tolerance to *B. inermis* enhanced when plants grew in soils from *B. inermis*-invaded areas relative to soils from uninvaded areas, indicating a lower competitive ability of *B. inermis* in its own soil (Stotz *et al.* 2018). Instead, we suggest that since *B. inermis* is a clonal species, the predominant vegetative reproduction through new tillers in the areas that accumulated stronger negative plant-soil feedbacks (Table 5) may be an important mechanism to transfer nutrients between ramets (Otfinowski and Kenkel 2008) allowing *B. inermis* to further invade native grasslands (Eviner 2004) while experiencing negative plant-soil feedbacks. Further studies testing for characteristics of invasive plant species in invaded areas would provide a better understanding of the mechanisms enabling them to invade the community under the conditions of negative plant-soil feedbacks.

4.2. The effect of time since introduction on resource availability and alternation of plant-soil feedbacks for B. inermis

Both biotic and abiotic factors of the invaded community have the potential to influence the effect of plant-soil feedbacks in the context of invasion (Smith - Ramesh *et al.* 2017; Bennett and Klironomos 2019). Here our results suggest a role for environmental factors in determining the dynamics of plant-soil feedbacks for *B. inermis* through changes in resource availability of invaded communities in relation to residence time. Consistent with previous studies on *B. inermis* invasion (Bennett and Cahill 2016; Stotz *et al.* 2019), phosphorus was found to increase in the areas that had been invaded longer (Figure 6) which ultimately resulted in the accumulation of stronger negative plant-soil feedbacks for *B. inermis* (Figure 7). Shifts in the strength and direction of plant-soil feedbacks in relation to phosphorus availability may be driven by reduced investment in defense, allelopathy and/or allocation to root tissue in high-nutrient soils patches (Coley *et al.* 1985), where more parasitic nutritional symbionts are expected to accumulate (Johnson *et al.* 1997; Kiers *et al.* 2007; Regus *et al.* 2014), thus favoring negative plant-soil feedbacks for *B. inermis*. However, increased phosphorus availability could also enhance *B. inermis* growth (via clonal growth and greater nutrient uptake capability) within invaded communities and hence decrease light availability over time (Figure 6; DeMalach *et al.* 2017). Decreasing light availability, as a result, was found to be associated with stronger and more negative plant-soil feedbacks for *B. inermis*, which is consistent with other findings on the effect of light on plant-soil feedback development. (McCarthy-Neumann and Ibáñez 2013; Smith and Reynolds 2015). Shading can limit carbon allocation to mutualists in *B. inermis*-invaded soils (Mangan *et al.* 2010; Pfennigwerth *et al.* 2018) and result in reduction of mycorrhizal biomass and root colonization over time (Guoxi *et al.* 2014; Konvalinková *et al.* 2015) increasing the cost of nutrient investment and shifting plant-soil feedbacks for *B. inermis* towards more negative. Yet, this was beyond the scope of our study and remains to be tested (Day *et al.* 2015). Alternatively, it is possible that decrease in light availability creates more favorable conditions for detrimental organisms of *B. inermis*-invaded communities (Augspurger and Kelly 1984; McCarthy-Neumann and Ibáñez 2013), further outweighing the effects of beneficial soil biota in the areas that had been invaded longer and negatively affecting the seedling performance of *B. inermis* (Figure 5; Otfinowski *et al.* 2007; Pfennigwerth *et al.* 2018). Interestingly, decreased light availability within the invaded community did not result in lower evapotranspiration over time, as no change in soil moisture was observed and as a result no association with accumulation of negative plant-soil feedbacks for *B. inermis* (Figure 6-7). While acknowledging limited sample size, we also not that the lack of difference in soil moisture is consistent with the previous study on resource availability following *B. inermis* invasion (Stotz *et al.* 2019) and although small differences among invaded areas may remain undetected, large differences are likely to be apparent even with low sample sizes. Likewise, while we expect higher pH levels in *B. inermis*-invaded soils that may directly contribute to soil microbial structure (Piper *et al.* 2015a, b), we found that pH does not necessarily change within invaded communities over time and was not linked to the accumulation of negative plant-soil feedbacks for *B. inermis* in the later stages of invasion.

We also acknowledge that soil properties measured here only represent a subset of environmental factors likely to influence the effect of plant-soil feedbacks. For example, Medina-Roldán *et al.* (2012) has demonstrated that herbivory may contribute to plant community structure while favoring grazing-adapted species via changes in resource availability. In addition, herbivory may also change soil physical characteristics of grazed pastures (Donkor *et al.* 2002) and induce sudden nutrient pulses through feces and urine (Early *et al.* 1998), which may alter not only soil microbial communities but also the local plant community. A detailed study of the potential impact of herbivory on the temporal dynamics of plant-soil feedbacks is needed. Furthermore, there is an urgent need for studies across diverse ecosystems to identify how plant-soil feedbacks respond to changing climatic variables, including temperature and precipitation (Putten *et al.* 2016).

4.3. The effect of temporal dynamics of plant-soil feedbacks for B. inermis on community structure of invaded areas

Temporal dynamics of plant-soil feedbacks for *B. inermis* were positively associated with lower *B. inermis* impact on co-occurring species diversity (Figure 8). Studies from other invaded communities have shown similar results (Dostál *et al.* 2013; Chung *et al.* 2019), yet the specific mechanisms underlying this relationship remain largely unknown. Here our work suggests that the strongest impact of *B. inermis* on community structure is exerted in the early stages of invasion, with the impact diminishing through the accumulation of more negative plant-soil feedbacks for *B. inermis* over time relative to plant-soil feedbacks that are neutral or weakly negative (Table 9-11; van der Putten and Peters 1997; Kardol *et al.* 2007). It is possible that stronger negative plant-soil feedbacks change plant competitive outcomes and hierarchies of *B. inermis*-invaded communities (Petermann *et al.* 2008; Stanescu and Maherali 2017) which could prevent competitive dominance of *B. inermis* and promote coexistence over time (Bever 2003; Bonanomi *et al.* 2005; Lekberg *et al.* 2018). Negative plant-soil feedbacks for *B. inermis* may also operate similarly to Janzen-Connell effects (Janzen 1970; Connell 1971), whereby *B. inermis* adults harbor host-specific soil enemies that reduce the success of juveniles in the invaded communities (Figure 5). Nevertheless, we also found that the other factors of the invaded community may overcome the effects of negative plant-soil feedbacks for *B. inermis* and slow down the recovery process (Table 9-11). The long-term impacts of *B. inermis* invasion on plant community structure were also mediated by the indirect effects of increased *B. inermis* litter production (Figure 8), typically associated with competitive exclusion and reduced community diversity (Piper *et al.* 2015a, b). Increased litter cover in *B. inermis*-invaded areas may not only suppress resident species through shading (Facelli and Pickett 1991; Xiong and Nilsson 1999; Lamb 2008; Loydi *et al.* 2013) but has been found to increase the input of organic substrates (Piper *et al.* 2015a, b) resulting in increased niche availability (Hooper *et al.* 2000; Zhou *et al.* 2002; Ramirez *et al.* 2010; Fierer and Lennon 2011) and more diverse microbial communities of invaded areas. This highlights the importance of assessing other drivers of the long-term dynamics and impacts of *B. inermis* invasion, as it would provide a better understanding of the mechanisms enabling species coexistence in *B. inermis*-invaded communities. For example, others have found that plant-scale spatial heterogeneity in plant-soil feedbacks can further promote species coexistence (Burns and Brandt 2014), as well as climate variability via fluctuation-dependent mechanisms such as the storage effects (Chesson 2000; Angert *et al.* 2009).

Knowing the direction and strength of plant-soil feedbacks for *B. inermis* and their impact on invaded communities can improve our understanding and ability to predict the outcomes of plant invasions. (Flory and Clay 2013). Since *B. inermis* accumulated negative plant-soil feedbacks over time but their effects were not strong enough to facilitate resident species recovery of invaded areas, the strategy used should focus on early detection and timely management strategies to prioritized sites with the shortest invasion history as restoration efforts in later invasion stages might be more costly and ultimately unsuccessful (Rejmánek and Pitcairn 2002; Norton 2009; Simberloff *et al.* 2013). Further, environmental context dependence of plant-soil feedback for *B. inermis* could also improve the management of invasive plants in grasslands by providing strongly place-based approaches that can offer “custom-fit” analyses and solutions for *B. inermis* invasion (Smith - Ramesh *et al.* 2017). By the identifying susceptibility of *B. inermis* to nutrient availability in invaded areas, we could alter soil conditions in a way to create less favorable interactions of *B. inermis* with invaded soils. Soil nutrient levels can be managed by altering soil microbial communities, grazing, mowing, and using different types of vegetation restoration (e.g. cover crops and bridge species) (Vasquez *et al.* 2008; Medina-Roldán *et al.* 2012). In addition, the reduction of biomass may also help to increase the impact of overtime accumulation of negative plant-soil feedbacks for *B. inermis* on biodiversity within the invaded community (Figure 8a, b; Oomes 1990; Maron and Jefferies 2001), and facilitate the recovery of resident species.

5. CONCLUSION

Understanding temporal dynamics of plant-soil feedbacks in the context of invasion is an important frontier in the development of this subfield. Our study has shown that at least in Alberta *B. inermis* accumulate stronger negative plant-soil feedbacks over time (Diez *et al.* 2010), while still being dominant within a community. As such, we suggest that some invasive species may invade native grasslands even in the presence of negative plant-soil feedbacks with allocation towards more vegetative reproduction, which may allow them to increase nutrient residence time within the plant and facilitate the invasion (Otfinowski and Kenkel 2008). In addition, detrimental soil microorganisms of invaded areas may not necessarily be the major drivers of accumulation of negative plant-soil feedbacks, as often suggested for temporal dynamics of plant-soil feedbacks in the context of invasion (Diez *et al.* 2010; Dostál 2011; Flory and Clay 2013). Further studies testing for other drivers of negative plant-soil feedbacks in relation to residence time would provide a better view on the mechanisms enabling species coexistence in invaded communities. Moreover, an improved understanding of environmental context dependence of plant-soil feedbacks can help us to predict under which conditions invasive species tend to experience more negative plant-soil feedbacks, allowing us to take advantage of invasive forage species while preventing/reducing their impact on biodiversity (Davis *et al.* 2010).

6. TABLES AND FIGURES

Table 1. Model Selection and Akaike's Information Criterion (AIC) to estimate *B. inermis* rate of expansion for each transect. The models examined in this study were: Linear ($y_i=\beta_0+\beta_1X_i+e_i$), Quadratic ($y_i=\beta_0+\beta_1X_i+ \beta_2X_i^2+e_i$), and Logarithmic ($y_i=\beta_0+\beta_1\ln(X_i)+e_i$), where the dependent variable was y (time since introduction), the independent variable was *B. inermis* abundance along the transect since 2013, β_0 and β_2 were the coefficients to be determined, and e_i is random error.

		Linear		Quadratic		Logarithmic	
Site	Transect	R^2	AIC	R^2	AIC	R^2	AIC
Kinsella	1	0.908	15.929	0.911	17.726	0.914	17.593
Kinsella	2	0.999	-11.630	0.998	-9.630	0.988	4.111
Kinsella	3	0.979	8.505	0.979	10.467	0.972	10.953
Kinsella	4	0.984	7.059	0.984	8.893	0.981	8.855
Kinsella	5	0.994	1.609	0.996	1.649	0.986	6.469
Kinsella	6	0.776	20.377	0.839	20.731	0.792	20.451
Kinsella	7	0.978	8.735	0.978	10.727	0.971	10.304
Mattheis	1	0.812	19.507	0.987	7.848	0.776	20.378
Mattheis	2	0.932	14.406	0.934	16.202	0.926	14.812
Mattheis	3	0.974	9.607	0.987	8.152	0.958	11.929
Mattheis	4	0.876	17.406	0.927	16.766	0.892	16.709
Mattheis	5	0.961	11.573	0.965	13.089	0.971	10.271
Mattheis	6	0.860	18.013	0.907	17.971	0.843	18.601

Table 2. Mean and standard deviation for all variables included in structural equation modeling analysis.

Variable	Mean ± standard deviation
Time since introduction	6.7 ± 4.78
Plant-soil feedback	-0.9 ± 1.46
B. inermis shoot biomass	410.7 ± 281.33
B. inermis litter biomass	1199.5 ± 711.42
Plant species richness	7.4 ± 3.03
Plant species evenness	0.8 ± 0.15
Non-brome shoot biomass	27.9 ± 20.68

Table 3. Chi-squared values (χ^2), Comparative Fit Index (CFI), Root Mean Square Error of Approximation (RMSEA), Standardized Root Mean Square Residuals (SRMR), and Akaike's Information Criterion (AIC) for all SEM models and recommended cut-offs that indicate a good fit.

	χ^2 ($p>0.05$)	CFI (≥90)	RMSEA (<0.08)	SRMR (<0.08)	AIC
Plant species richness	0.043	0.970	0.221	0.043	-428.914
Plant species evenness	0.040	0.953	0.211	0.044	-534.448
Non-brome shoot biomass	0.037	0.970	0.202	0.044	-428.316

Table 4. Linear mixed models, testing for temporal dynamics of plant-soil feedbacks for *B. inermis.* Feedback was calculated as the log response ratio: (a) For whole-soil approach - ln[biomass(full treatment) / biomass(control treatment)], (b) For inoculum approach - ln[biomass(inoculum treatment) / biomass(no inoculum treatment)].

	df	F	p-value
Whole-soil approach	1, 303	29.75	<0.0001
Inoculum approach	1, 300	0.51	0.47

Table 5. Linear mixed models, relating negative plant-soil feedbacks for *B. inermis* to population performance of *B. inermis* in natural systems. Feedback was calculated as the log response ratio for whole-soil approach - ln[biomass(full treatment) / biomass(control treatment)].

	df	F	p-value
Shoot cover (g/m2)	1,137	22.05	<0.0001
Litter cover (g/m2)	1,296	1.06	0.31
Number of tillers	1,297	12.78	<0.01
Reproductive effort	1,134	3.98	0.05

Table 6. Linear mixed models, relating the interaction of time since introduction with resource availability of *B. inermis* invaded areas.

	df	F	p-value
Light transmission	1,90	7.21	<0.01
Soil Moisture	1,90	0.12	0.72
pH	1,89	1.67	0.19
Phosphorus	1,88	23.51	<0.01

Table 7. Linear mixed models, testing for the effect of resource availability of *B. inermis*-invaded areas on the dynamics of plant-soil feedbacks for *B. inermis.* Feedback was calculated as the log response ratio for whole-soil approach - ln[biomass(full treatment) / biomass(control treatment)].

	df	F	p-value
Light transmission	1,61	3.67	0.05
Soil Moisture	1,16	1.15	0.29
pH	1,36	2.61	0.11
Phosphorus	1,31	4.81	0.03

Table 8. Linear mixed models, testing for the effect of resource availability of *B. inermis*-invaded areas on the dynamics of microbially mediated plant-soil feedbacks for *B. inermis*. Feedback was calculated as the log response ratio for inoculum approach - ln[biomass(inoculum treatment) / biomass(no inoculum treatment)].

	df	F	p-value
Light transmission	1,294	0.06	0.79
Soil Moisture	1,294	0.05	0.83
pH	1,294	0.01	0.91
Phosphorus	1,294	0.14	0.70

Table 9. Structural equation modeling (SEM) results for total, direct, and indirect effects of *B. inermis* invasion on plant species richness of invaded communities. Standardized estimates are shown, in bold if significant (* p-value < 0.05, ** p-value < 0.01).

	Path Coefficients			
	To plant species richness (SR)	To plant-soil feedbacks for *B. inermis* (PSF)	To *B. inermis* shoot biomass (SB)	To *B. inermis* litter biomass (LB)
Time since introduction (TSI)	**-0.007****	**-0.011****	0.005	**0.009****
Plant-soil feedbacks for *B. inermis* (PSF)	**-0.131***		-0.003	-0.003
B. inermis shoot biomass (SB)	**-0.269****			**-0.019****
B. inermis litter biomass (LB)	**-0.443****			

	Indirect effects			
	Estimate (b)	Standard error	LLCI	ULCI
Total indirect effect	**-0.011****	0.003	-0.016	-0.006
TSI → PSF → SR	**0.001***	0.001	0.000	0.003
TSI → SB → SR	-0.001	0.001	-0.003	0.000
TSI → LB → SR	**-0.004****	0.001	-0.006	-0.001
TSI → PSF→ SB → SR	-0.000	0.000	0.000	0.000
TSI → PSF → LB → SR	-0.000	0.000	0.000	0.000

Table 10. Structural equation modeling (SEM) results for total, direct, and indirect effects of *B. inermis* invasion on plant species evenness of invaded communities. Standardized path coefficients are shown, in bold if significant (* p-value < 0.05, ** p-value < 0.01).

	Path Coefficients			
	To plant species evenness (SE)	To plant-soil feedbacks for *B. inermis* (PSF)	To *B. inermis* shoot biomass (SB)	To *B. inermis* litter biomass (LB)
Time since introduction (TSI)	-0.003	__-0.011__**	0.005	__0.009__**
Plant-soil feedbacks for *B. inermis* (PSF)	__-0.125__**		-0.003	-0.003
B. inermis shoot biomass (SB)	-0.062			__-0.019__**
B. inermis litter biomass (LB)	__-0.127__**			

	Indirect effects			
	Estimate (b)	Standard error	LLCI	ULCI
Total indirect effect	-0.003	0.001	-0.007	0.001
TSI → PSF → SE	__0.001*__	0.00	0.000	0.002
TSI → SB → SE	-0.000	0.001	-0.001	0.000
TSI → LB → SE	__-0.001*__	0.000	-0.002	0.000
TSI → PSF→ SB → SE	-0.000	0.000	0.000	0.000
TSI → PSF → LB → SE	-0.000	0.002	0.000	0.000

Table 11. Structural equation modeling (SEM) results for total, direct, and indirect effects of *B. inermis* invasion on non-brome shoot biomass of invaded communities. Standardized path coefficients are shown, in bold if significant (* p-value < 0.05, ** p-value < 0.01).

	Path Coefficients			
	To non-brome shoot biomass (NB)	To plant-soil feedbacks for *B. inermis* (PSF)	To *B. inermis* shoot biomass (SB)	To *B. inermis* litter biomass (LB)
Time since introduction (TSI)	**-0.022****	**-0.011****	0.005	**0.009****
Plant-soil feedbacks for *B. inermis* (PSF)	**-0.154****		-0.003	-0.003
B. inermis shoot biomass (SB)	**-0.243****			**-0.019****
B. inermis litter biomass (LB)	0.041			

	Indirect effects			
	Estimate (b)	Standard error	LLCI	ULCI
Total indirect effect	**-0.021****	0.002	-0.026	-0.017
TSI → PSF → NB	**0.002***	0.001	0.000	0.003
TSI → SB → NB	-0.001	0.000	-0.003	0.000
TSI → LB → NB	0.000	0.000	-0.001	0.001
TSI → PSF→ SB → NB	-0.000	0.000	0.000	0.000
TSI → PSF → LB → NB	-0.000	0.000	0.000	0.000

Figure 1. Field sampling design. (a) Line-intercept transects were used to encompass the transition between *B. inermis*–invaded areas (blue arrow) to native-dominated areas (red arrow), continuously monitored since 2013 by the Cahill Lab of Experimental Plant Ecology. (b) The modified belt-transect method was used to measure recourse availability along the transect and community structure (species richness, species evenness and non-brome biomass), and to collect soils to be used as a living inoculum in a greenhouse experiment.

(a)

(b)

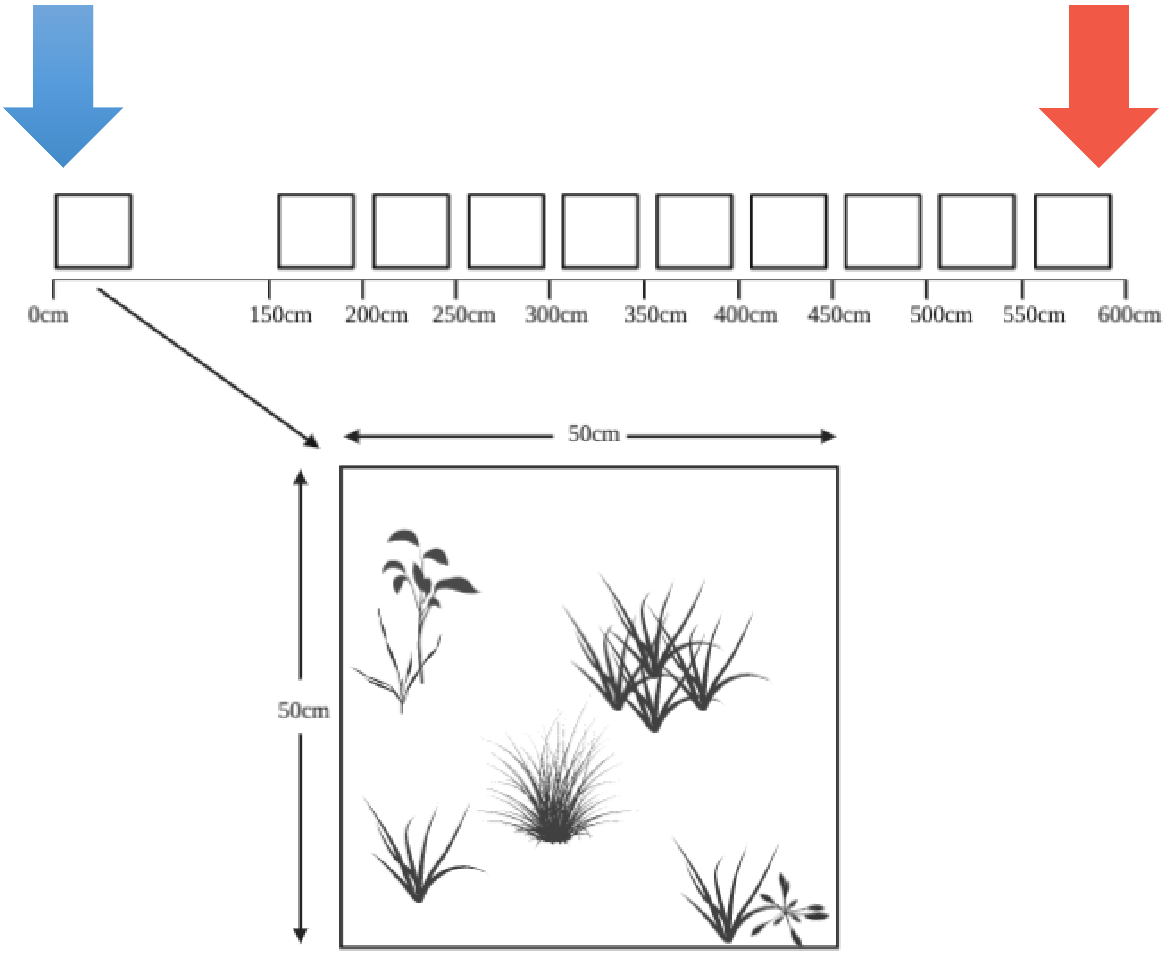

0cm
150cm
200cm
250cm
300cm
350cm
400cm
450cm
500cm
550cm
600cm
50cm
50cm

Figure 2. Greenhouse experiment. Phase 1: The conditioning phase took place in the field. Phase 2: *B. inermis* response to inoculum from each sampling position. For the whole-soil approach (*), *B. inermis* biomass was compared between full inoculum treatment and control treatment. For inoculum soil approach (**), *B. inermis* biomass was compared between inoculum treatment and no inoculum treatment, with both having a 9:1 mixture of potting soil and living inoculum.

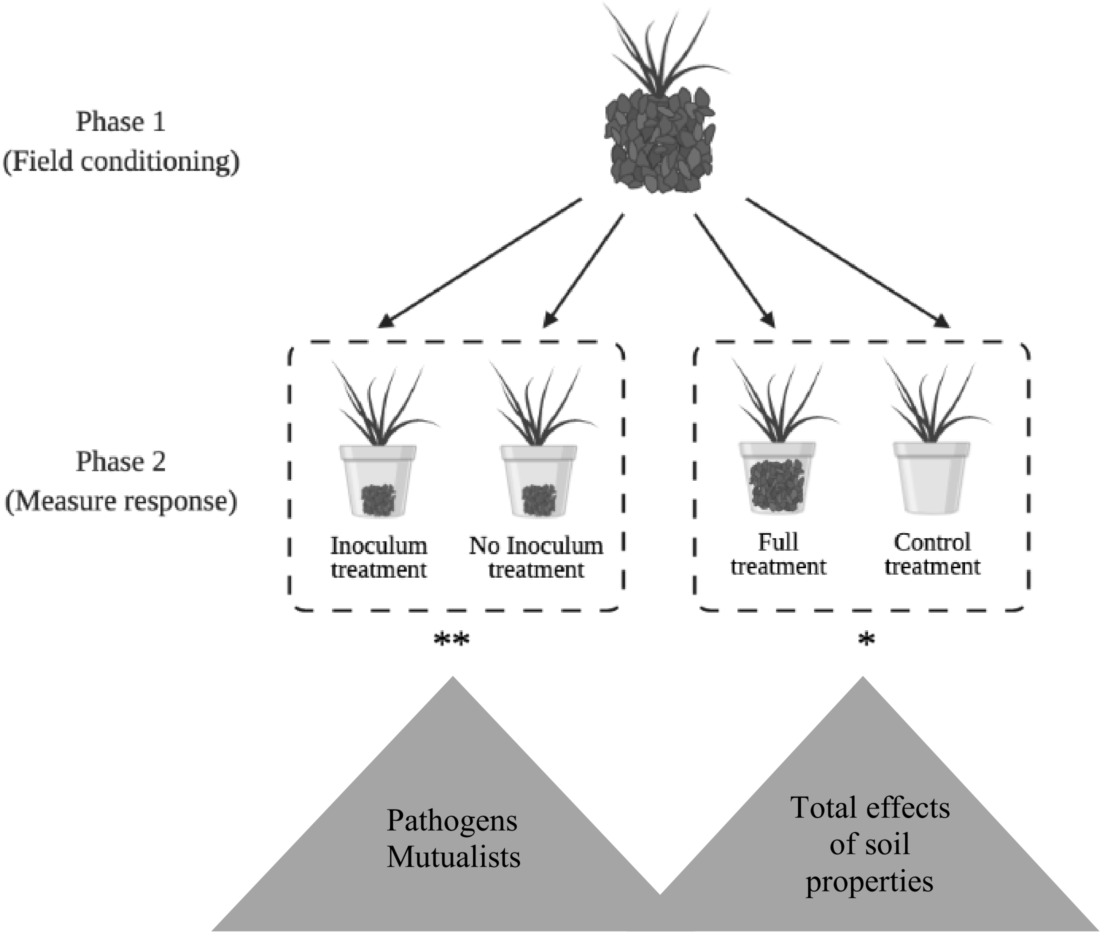


Figure 3. Initial structural equation model and mediation pathway for the long-term dynamics and impacts of *B. inermis* invasion on plant community structure.

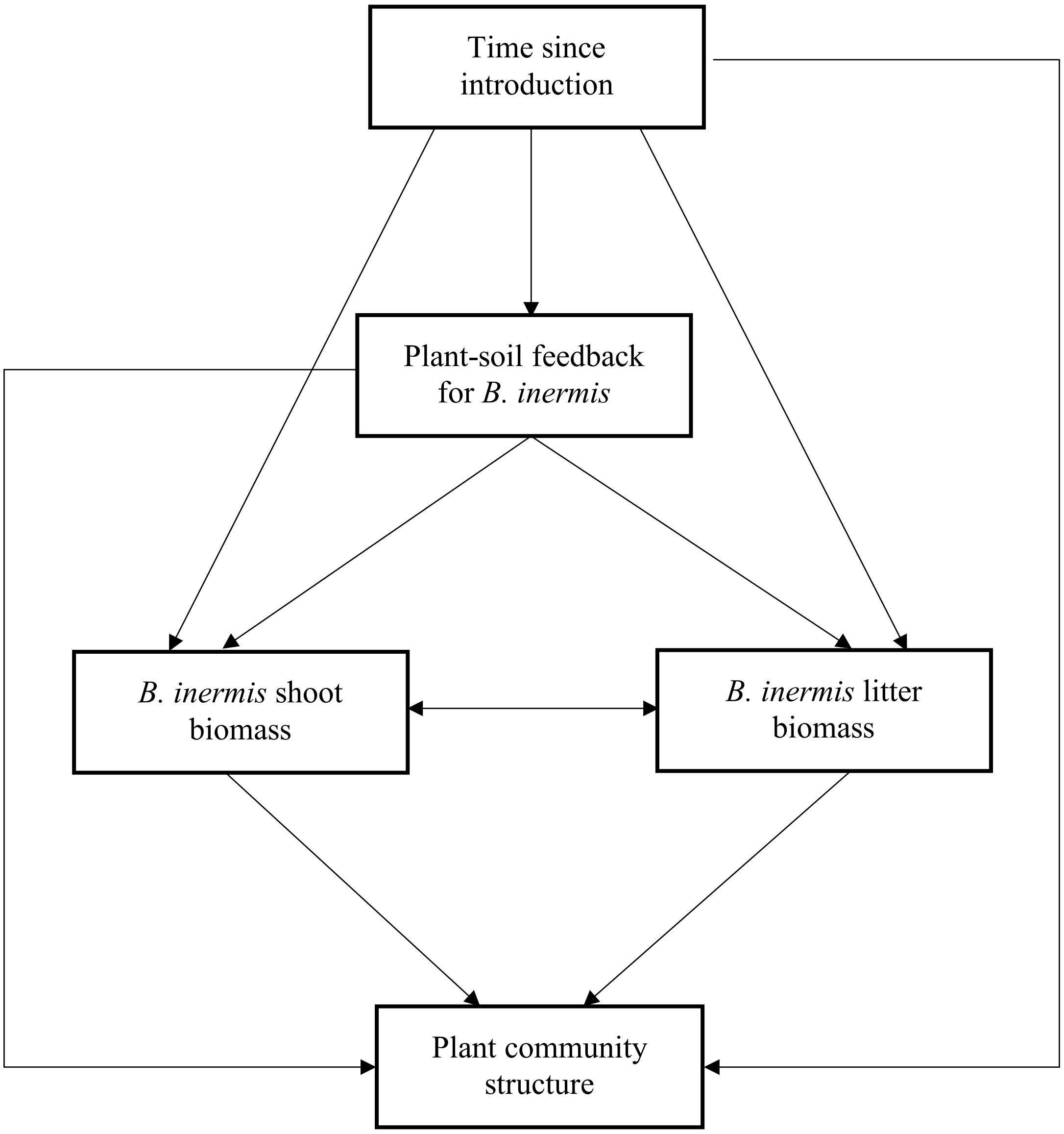


Figure 4. The strength and direction of plant-soil feedbacks for *B. inermis* as a function of time since introduction by *B. inermis* into the range. Feedback was calculated as the log response ratio: (a) For whole-soil approach - ln[biomass(full treatment)/ biomass(control)], (b) For inoculum approach - ln[biomass(inoculum treatment)/ biomass(no inoculum)].

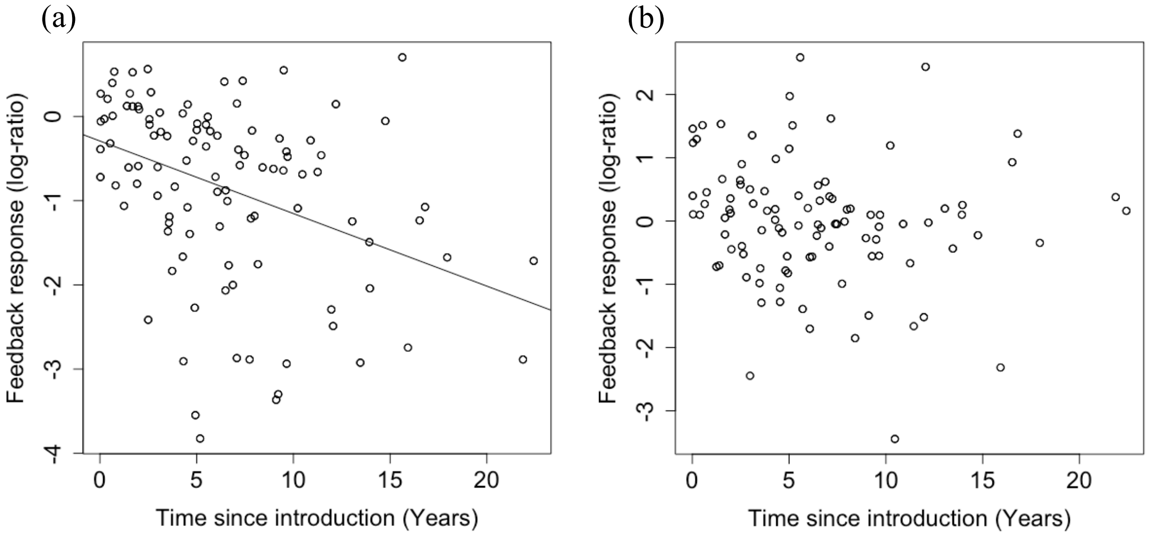


Figure 5. The effect of temporal dynamics of plant-soil feedbacks for *B. inermis* on population growth of *B. inermis* in natural systems.

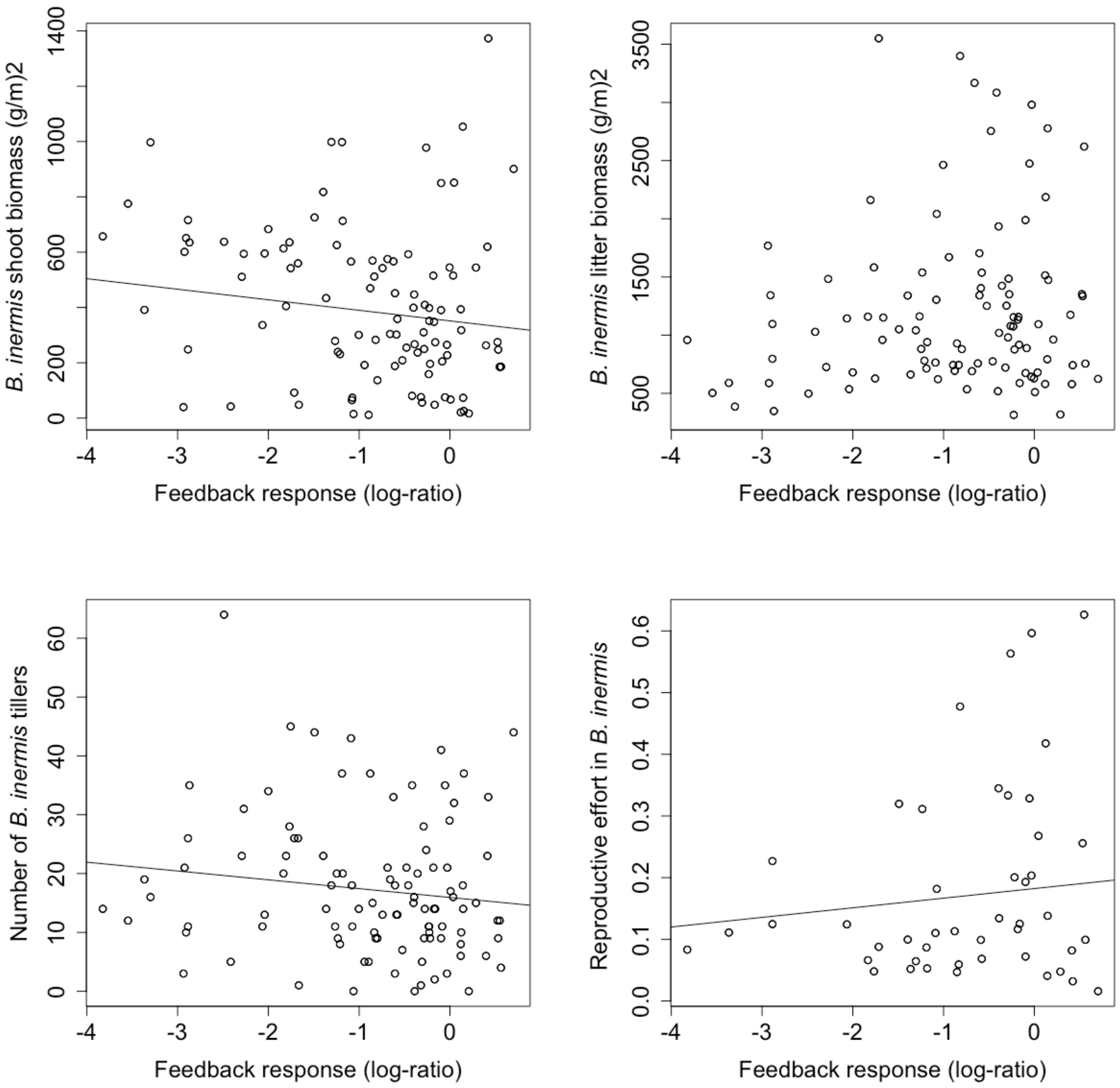


Figure 6. The interaction of time since introduction with resource availability of *B. inermis*-invaded areas.

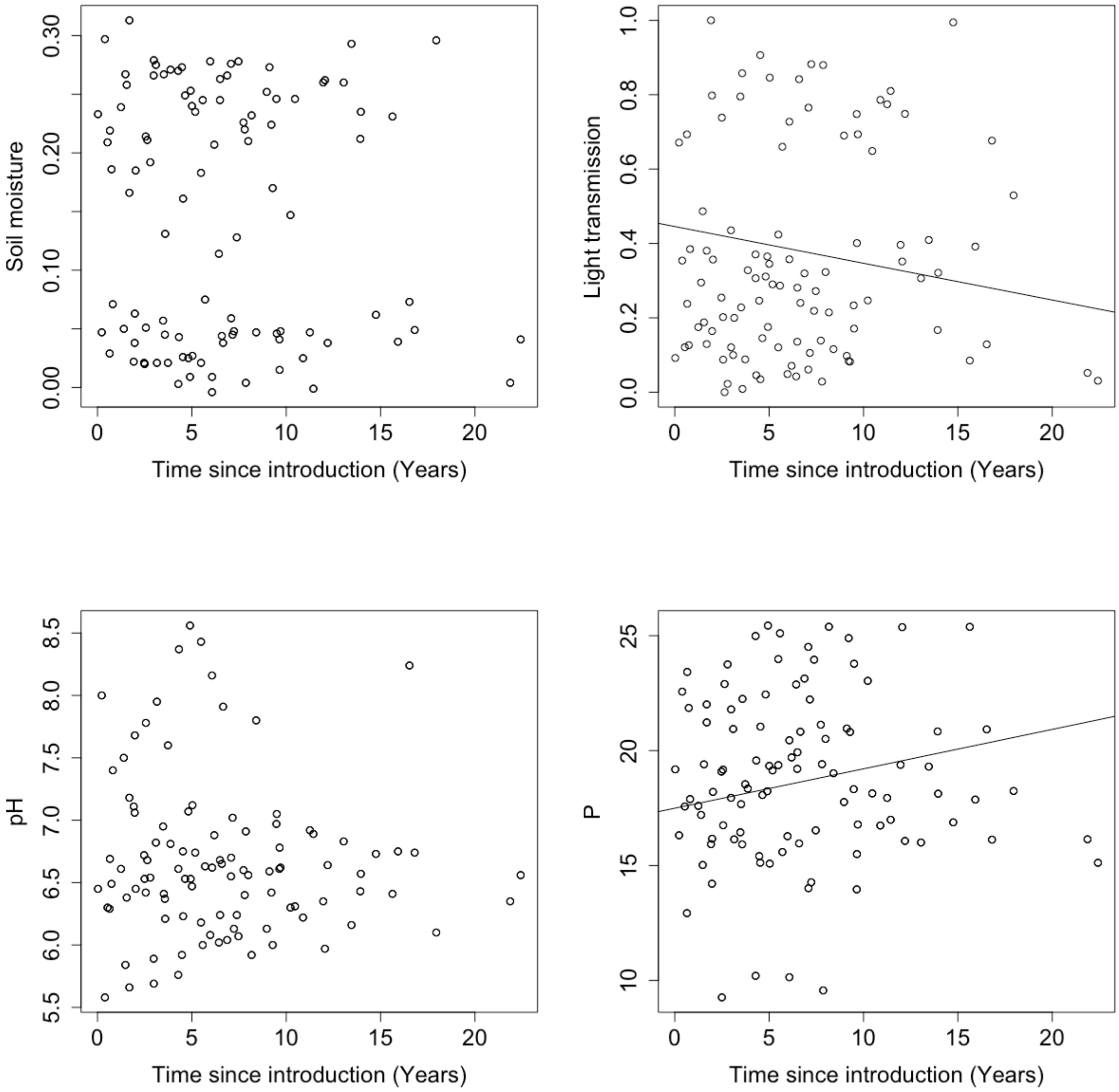


Figure 7. The effect of resource availability of *B. inermis*-invaded areas on temporal dynamics of plant-soil feedbacks for *B. inermis.* Feedback was calculated for whole-soil approach - ln[biomass(full treatment)/ biomass(control treatment)].

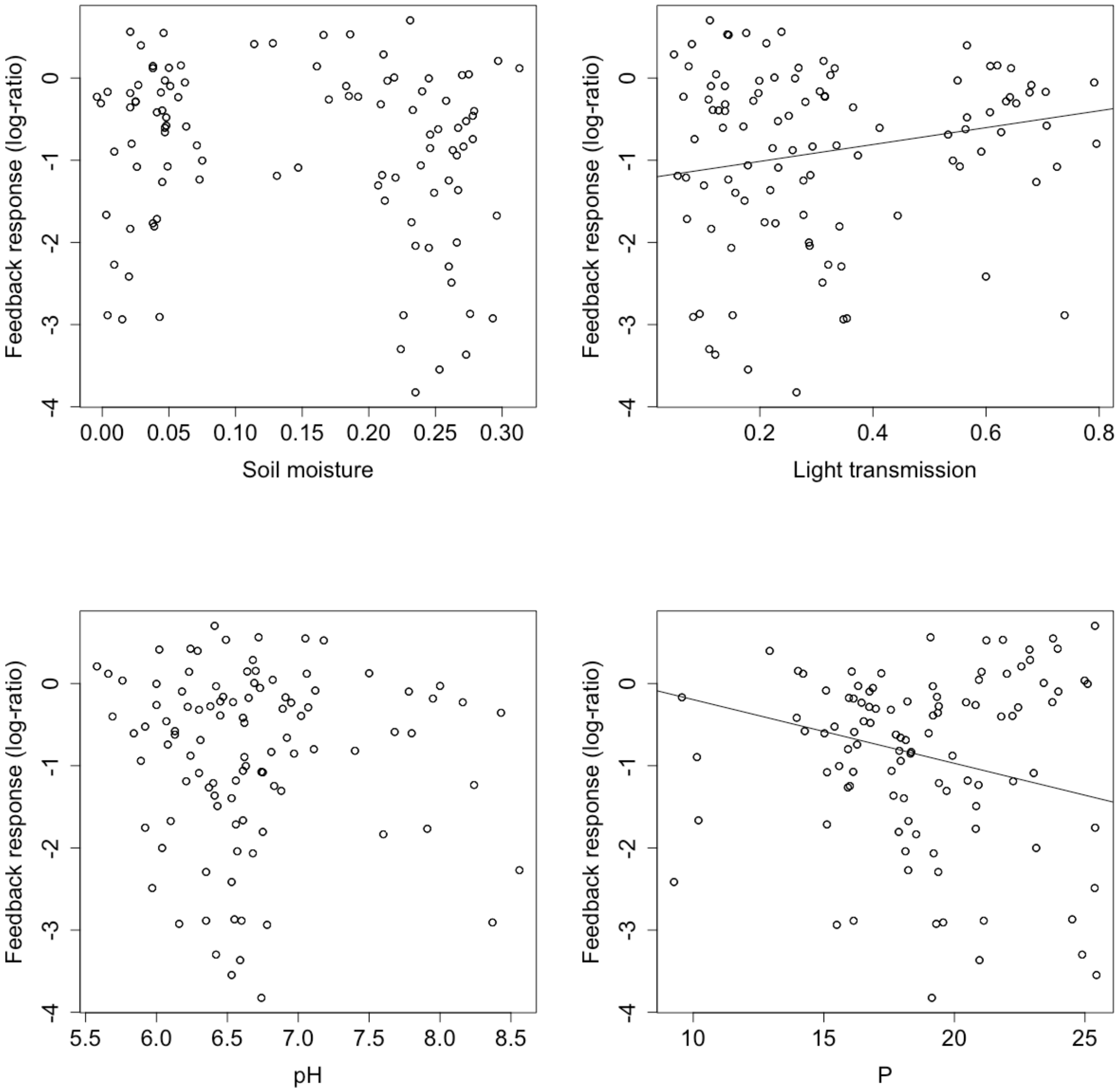
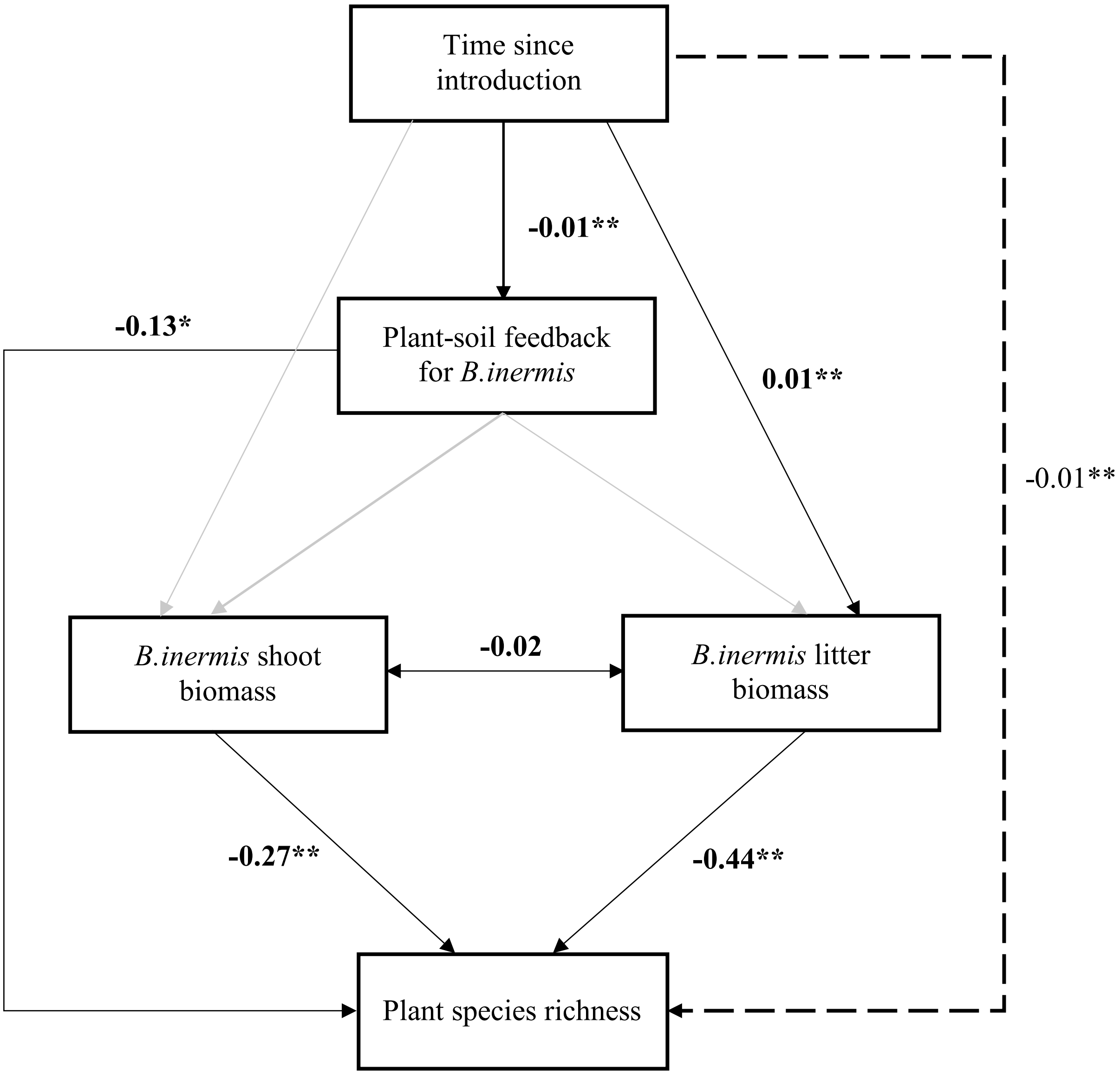
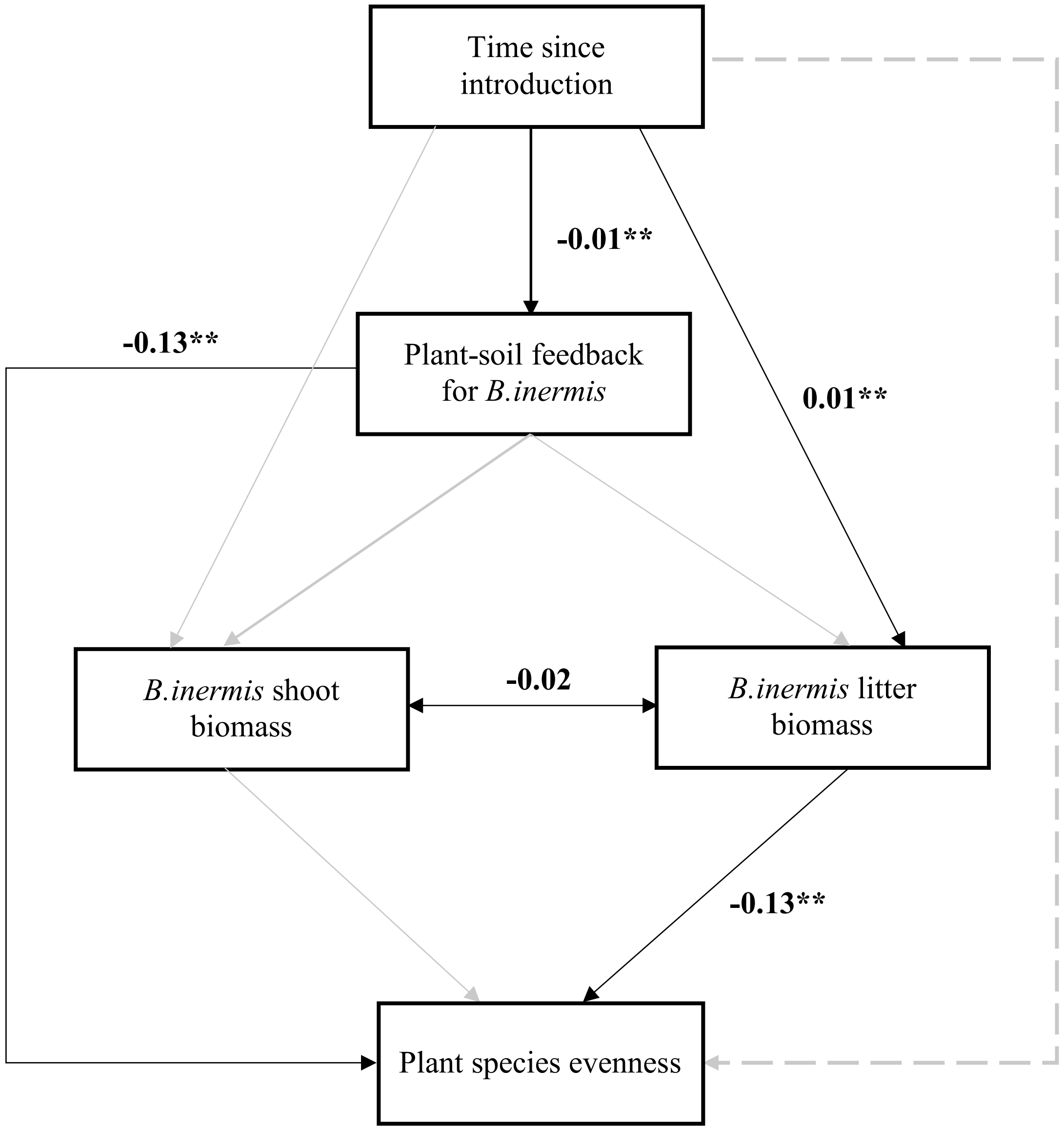


Figure 8. Structural equation models for the long-term impacts of *B. inermis* invasion on (a) plant species richness, (b) plant species evenness, (c) non-brome biomass. Direct relationship from time since introduction and plant community aspect is shown as dashed line, and solid lines represent indirect mediation effect. Black arrows represent significant relationships (* p-value < 0.05, ** p-value < 0.01), and grey lines represent non-significant relationships. Standardized path coefficients are shown next to significant pathways.

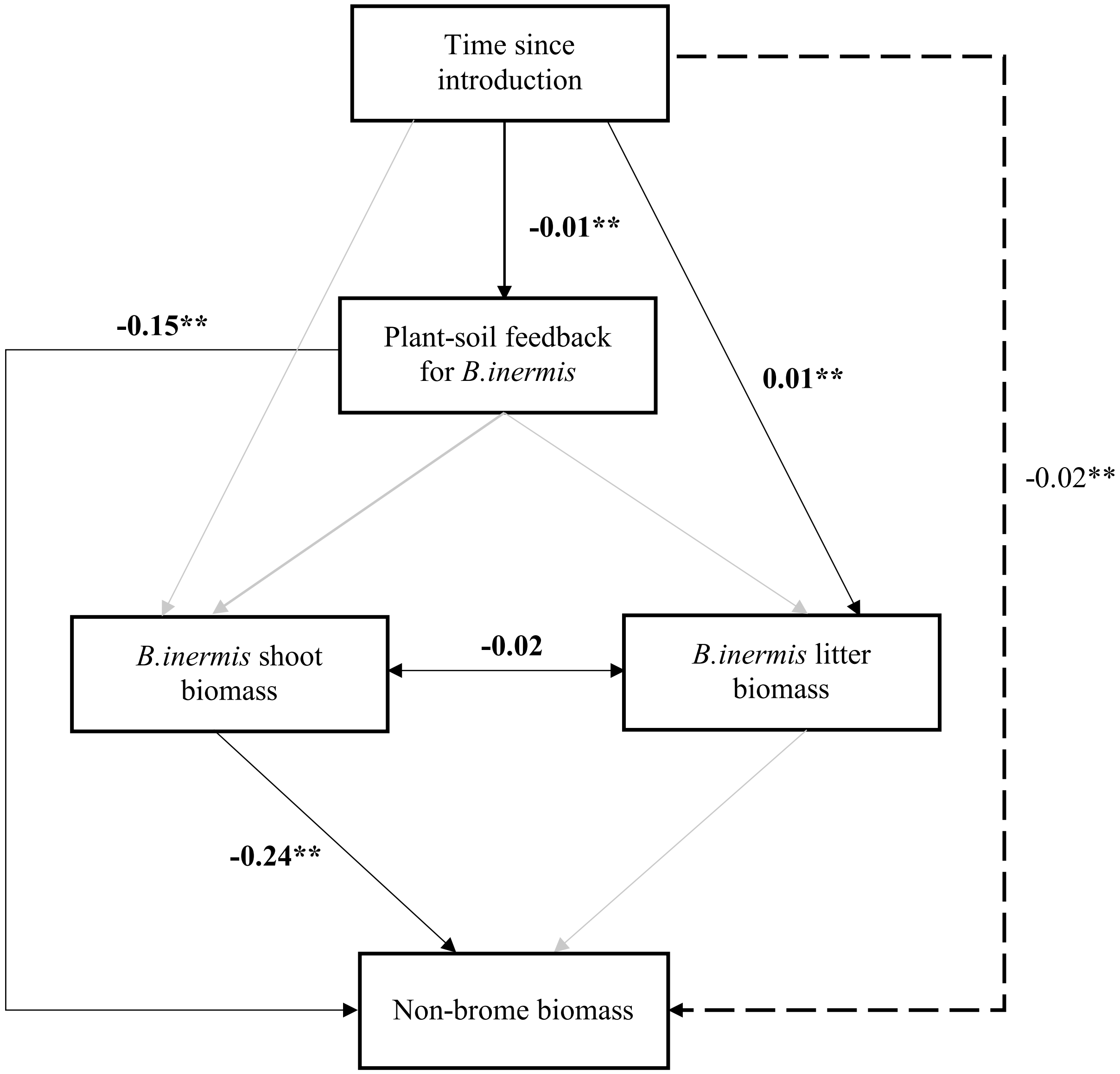
(a)



(b)


Time since introduction
-0.01**
-0.13**
Plant-soil feedback for *B.inermis*
0.01**
B.inermis shoot biomass
-0.02
B.inermis litter biomass
-0.13**
Plant species evenness

(c)


Time since introduction
-0.01**
Plant-soil feedback for *B.inermis*
-0.15**
0.01**
-0.02**
B.inermis shoot biomass
-0.02
B.inermis litter biomass
-0.24**
Non-brome biomass

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