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RESEARCH ARTICLE

Effect of soil carbon amendments in reversing the legacy effect of plant invasion

Ziliang Zhang¹ | Prasanta C. Bhowmik² | Vidya Suseela¹

¹Department of Plant & Environmental Sciences, Clemson University, Clemson, SC, USA

²Stockbridge School of Agriculture, University of Massachusetts, Amherst, MA, USA

Correspondence Vidya Suseela Email: vsuseel@clemson.edu

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Abstract

- 1. Invasive plants are key drivers of global environmental changes leading to the disruption of ecosystems. Many invasive species engage in novel niche construction through plant-soil feedbacks that are driven by plant secondary compounds. These compounds can persist in the soil even after removing the invader, thus creating a legacy effect that inhibits the return of native flora and fauna. The formulation of active intervention strategies that can reverse niche construction is therefore critical for the restoration of these invaded ecosystems.
- 2. We conducted this study in an old-field in Massachusetts, USA, that has been invaded by Japanese knotweed (Polygonum cuspidatum) for >20 years. We chose knotweed as a model system as it alters soil chemistry and microbial community through the input of polyphenols such as tannins that creates a legacy effect. Following the removal of knotweed biomass, we investigated the effect of two soil carbon (C) amendments (biochar and activated carbon) on the growth and establishment of newly seeded native and prairie species. We measured the percent plant cover and above-ground biomass to assess the establishment of the native and prairie species. We also measured soil and microbial characteristics including nutrient availability, extracellular enzyme activities and fungal biomass to elucidate the effect of C amendments in reversing the legacy effect.
- 3. Eventhough the native species did not respond positively to C amendments, the biomass of the prairie species was 80% higher in activated carbon and biochar amended plots than the non-amended control plots. The nitrate content of the C amended plots was five times higher than the non-amended plots indicating an increased N mineralisation in the C amended plots. This could be potentially due to the amelioration of phenolic compounds by activated carbon and biocharthrough sorption. The phenol peroxidase activity also increased in the activated carbon and biochar amended plots potentially due to the less inhibition by phenolic compounds. With the decrease in polyphenols, the fungal biomass decreased in C amended plots that may have resulted in faster nutrient cycling and increased availability of soil N.
- 4. Synthesis and applications. The phenolic compounds from the litter of invasive species that persist in soil C fractions can negatively affect the germination and

growth of the native or non-invasive plant species. The polyphenols such as tannins from the litter can complex nitrogenous compounds in soils making the N unavailable to the native or non-invasive species. Our results revealed the potential of soil C amendments in reversing niche construction and legacy effects of polyphenolrich invasive species and indicated that biochar could be a more economically feasible alternative to activated carbon in restoring invaded ecosystems. These results also emphasise thatunderstanding the mechanisms through which invasive species create a legacy effect is pivotal in formulating suitable knowledge-based practices for restoring invaded ecosystems.

KEYWORDS

activated carbon, biochar, Japanese knotweed, legacy effect, niche construction, phenolic compounds, plant invasion, restoration

1 | INTRODUCTION

Non-native invasive plant species (NIPS) are key drivers of global environmental changes as they disrupt the processes and services of the ecosystems they invade. The current success of NIPS coupled with their potential for range expansion with changing climate (Diez et al., 2012; Sorte et al., 2013) makes invasion one of the gravest threats to ecosystems in a future world. Apart from reducing the biodiversity and causing tremendous economic loss, many invasive species are ecosystem engineers that create novel niches through changes in the biotic and abiotic properties of the ecosystems. These novel niches persist for longer time-scales and often prevent the re-establishment of native species even after the removal of NIPS. This invader-induced change in ecosystem properties that persist even after removing the invasive species is termed as 'legacy effect' or 'ghost effect' (Kulmatiski, Beard, & Stark, 2006; Malcolm, Bush, & Rice, 2008; Suseela, Alpert, Nakatsu, Armstrong, & Tharayil, 2016). The legacy effect mediated through plant-soil feedbacks often results in failure of the restoration of invaded habitats (Kulmatiski et al., 2006). Although plant-soil feedbacks have been studied extensively from an invasion context, restoration practices that are based on a mechanistic understanding of the plant-soil feedbacks are seldom formulated.

The NIPS often create a legacy effect through changes in soil properties that would positively feedback to NIPS and negatively to native species. Plant-soil feedbacks, widely implied in the success of many invasive species (Reinhart & Callaway, 2006), refer to those processes by which plants alter the soil biological, chemical and structural properties (Ehrenfeld, 2003; Miki, 2012). These changes would provide NIPS with uncontested access to limiting soil resources and thus a competitive advantage over the native species (Pringle et al., 2009; Tharayil, Alpert, Bhowmik, & Gerard, 2013). Apart from changes in the microbial community and soil nitrogen (N) cycling, the NIPS also successfully engage in plant-soil feedbacks by altering soil carbon (C) cycling (Tamura, Suseela, Simpson, Powell, & Tharayil, 2017). This is often achieved through the input of litter which is chemically distinct from that of the native species, which further alters the composition and function of microbial communities and hence the rate of biogeochemical cycling (Elgersma, Yu, Vor, & Ehrenfeld, 2012; Farrer & Goldberg, 2009; Miki & Kondoh, 2002). For example, the input of labile (low C:N) litter by invasive species increased N cycling (Evans, Rimer, Sperry, & Belnap, 2001; Farrer & Goldberg, 2009) while the input of recalcitrant litter (high C:N, high lignin) decreased N content and altered the seasonality of N cycling (Drenovsky & Batten, 2007; Tharayil et al., 2013) to benefit the NIPS over their native counterparts.

The input of relatively recalcitrant litter would also select for fungal communities that would lower litter decomposition rate and would result in the persistence of several C compounds, which can alter soil C cycling. Certain groups of C compounds or microbial transformation products of these compounds in plant litter can persist in soils for longer time-scales, which could be highly instrumental in creating a legacy effect (Suseela et al., 2016). An important class of compounds in plant litter that can potentially create a legacy effect through changes in soil C chemistry are the plant secondary metabolites, particularly the phenolic compounds. Many of these phenolic compounds are involved in a wide range of physiological functions related to plant survival and fitness (Lattanzio, Kroon, & Quideau, 2008). However, these phenolic compounds persist in the senesced plant tissues and once they reach the soil, their inherent recalcitrance and biological functional activity can create a legacy effect by their long-term persistence and by changing the microbial community composition and enzyme activities (Northup, Yu, Dahlgren, & Vogt, 1995; Suseela & Tharayil, 2018). Negating the effect of these C compounds through active intervention methods is critical in reversing the legacy effect and restoring invaded habitats.

Currently, most of the efforts for restoring invaded ecosystems are focused primarily on selecting native species with traits similar or superior to invasive species. However, such efforts of restoration of invaded habitats reported mixed results (Von Holle & Simberloff, 2004). Also, common management practices, such as mechanical removal, herbicide treatments, prescribed burning or native species reintroduction (Glass, 2004; Nsikani, van Wilgen, & Gaertner, 2018), may not be sufficient for effective restoration due to the possibility of persistent impacts from the invader-induced soil legacy effects. In the context of reversing soil legacy effects, soil-based management approaches could provide necessary tools for restoring invaded sites to conditions that favour native species. The intentional application of C amendments to the soil is an active management practice involving soil manipulation that could reduce the growth of invaders (Corbin & D'Antonio, 2012; Kulmatiski et al., 2006). Activated carbon has been used as a restoration tool in invaded habitats due to its ability to bind organic compounds and mediate plant-soil feedbacks (Kulmatiski, 2011: Nolan, Kulmatiski, Beard, & Norton, 2015). However, the effect of activated carbon addition on reversing soil properties and legacy effect under field conditions is seldom investigated. Furthermore, research focusing on comparing the efficiency of activated carbon to other similar soil amendments such as biochar, which is economically more feasible is much limited.

In this study, we selected Japanese knotweed (Polygonum cuspidatum) as a model species to study the effect of active soil intervention measures such as activated carbon and biochar to restore the invaded habitats. Japanese knotweed is a perennial, herbaceous plant species native to eastern Asia and is now problematic in 45 states in the US. Japanese knotweed is an ideal species to test these soil amendment practices as knotweed input litter rich in recalcitrant compounds that decompose slowly compared to the native species or other invaders with more labile litters (Tamura & Tharayil, 2014). The input of recalcitrant knotweed litter results in the accumulation of a dense detritus layer in the invaded stands (Maurel et al., 2010) that further altered soil C cycling (Tamura et al., 2017), increased fungal biomass and composition and microbial functional activity (Suseela et al., 2016). Knotweed litter (root and shoot) has a high C/N ratio (>140:1) and is abundant in lignin and polyphenols including tannins and flavonoids that may retard the microbial decomposition (Tamura & Tharayil, 2014). Our recent research revealed that soils under knotweed invaded stands contained twice as much phenolics as the adjacent non-invaded soils

and the composition of phenolics also differed between the invaded and non-invaded stands (Suseela et al., 2016). The formation of microbial transformation products of plant heteropolymers such as lignin also contributes to the persistence of recalcitrant phenolic compounds in soils under knotweed invaded stands (Suseela et al., 2016; Tamura et al., 2017). These phenolic compounds tend to persist and accumulate in soils long after the removal of the invasive species and can negatively affect the germination and growth of native species and can lead tofailure in the restoration of invaded habitats. Active restoration practices can help in the reversal of soil legacy effect compared to passive restoration which relies on natural succession after the removal of the invader. We hypothesised that management practices that can reverse the soil nutrient and microbial characteristics in the invaded ecosystems could facilitate the rapid restoration of the invaded sites. We predicted that adding soil C amendments could alter the soil microbial composition, functional activity and nutrient cycling facilitating the growth of native or non-invasive species.

2 | MATERIALS AND METHODS

2.1 | Study site and study species

The study site was selected in Amherst, Massachusetts (42°24'N, 72°31'W) as this site has been under knotweed invasion for more than 20 years (Barney, Tharayil, & DiTommaso, 2006; Suseela et al., 2016; Tharayil et al., 2013; Figure 1A). Previous research conducted at the same study site has compared the quantity and chemical composition of litter inputs between knotweed invaded and adjacent non-invaded sites (Tamura & Tharayil, 2014). Specifically, the shoot biomass of litter inputs in the knotweed-invaded site was three times higher than that in the adjacent non-invaded site. Moreover, the abundance of phenolic compounds detected in knotweed litter was higher than that of the native species in the adjacent non-invaded site (Suseela et al., 2016).



FIGURE 1 Japanese knotweed (*Polygonum cuspidatum*) in the study site (A), preparation of the study site for the restoration experiment (B, C) and cross section of a knotweed rhizome from the cleared area (D)

Particularly, the tannins could hardly be detected in native species, while it accounted for ~10% of knotweed litter biomass (Tharayil et al., 2013). Previous research conducted at the same study site has thus revealed that the input of a disproportionate quantity of knotweed biomass with contrasting litter chemistry than the native species creates an N deficiency that affects the growth of the native species (Tharayil et al., 2013), changes the quantity and composition of soil C and microbial community and functional activity under the invaded sites (Tamura et al., 2017; Tamura & Tharayil, 2014) ultimately leading to a legacy effect that prevents the re-establishment of the native species (Suseela et al., 2016).

2.2 | Experimental design

The study site for the restoration experiment was prepared in fall 2011 by first clearing the above-ground biomass of knotweed and the decomposing stems from the site (Figure 1). Rhizomes of knotweed were then removed to a depth of 30-35 cm by spot digging, and the holes were filled with the same soil to avoid extensive disturbance. In the cleared site, we demarcated 36 plots of 2 m \times 2 m and assigned the treatments in a randomised block design (three soil amendment treatments \times two plant species mixtures \times six replicates). Plots were separated from each other by a 40-cm buffer strip. Wooden planks were laid along the buffer strip of six blocks to access the individual plots. The treatments included two soil C amendments (activated carbon and biochar) and control plots devoid of any amendment and each treatment had six replicates. Biochar was obtained from southern yellow pine wood chips that were pyrolysed at a temperature between 550 and 700°C. The biochar had an internal absorption ratio of 250 cm²/cm³. The activated carbon type was DARCO G-60 with 100-mesh particle size and a surface area of 600 m^2/g (ACROS Organics, Fisher Scientific, USA). Activated carbon and biochar were applied at a rate (2% of soil volume) of 400 and 350 g/m², respectively, and were mixed with the top 5-cm soil. The control plots were raked to have a similar disturbance as that of the C amended plots. We added a mixture of native seeds consisting of Anemone virginiana (1 g/m^2) , Desmodium canadense (4 g/m^2) , Lespedeza capitata (2.5 g/m^2) , Aster ericoides (0.5 g/m²) and Andropogon gerardii (1 g/m²) to 18 plots. As prairie restoration is increasingly being advocated as a successful practice to reduce invasive species abundance (Blumenthal, Jordan, & Svenson, 2005; Larson et al., 2013), we added a mixture of prairie seeds consisting of Trifolium pratense (5.5 g/m²), Dactylis glomerata (7 g/m²), Lolium perenne (5.5 g/m²) and Vicia villosa (20 g/m²) to the other 18 plots.

2.3 | Measurements

2.3.1 | Percent cover and biomass

To assess the establishment of native and prairie species in different treatments, we measured the percent plant cover and above-ground biomass production in the 36 plots. The measurements were taken in June 2012 and 2013 when the above-ground growth was at or near the maximum. In each plot, measurements were taken from two spots using a quadrat of $0.5 \text{ m} \times 0.5 \text{ m}$. The biomass within the quadrat was cut at ground level and dried at 70°C for 48 hr and weighed. For biomass measurements, we avoided plots where native seeds were sown as the germination rate and growth of the native species were very low. In each plot, we also measured the number of knotweed shoot emergence and the emerging shoots were cut periodically from all the treatments.

2.3.2 | Soil sampling

In June 2013, we collected soils from the 18 plots where prairie seeds were added. From each plot, after removing the surface litter layer, four soil cores were collected to a depth of 0–10 cm. The four soil cores were composited to form a single representative sample from each plot and placed in a plastic bag on dry ice and shipped immediately to Clemson University. Upon receiving, the samples were stored at –20°C until analysis. The soils were subjected to the following analyses.

2.3.3 | Ergosterol (fungal biomass indicator)

Ergosterol is widely used as a fungal biomarker as it is the major sterol in fungi. Ergosterol in the soils was quantified as per Gessner and Schmitt (1996). We measured fungal biomass as opposed to total microbial biomass since our previous studies from the same study site and multiple knotweed invaded sites across the eastern US have indicated that knotweed invasion increased the abundance and composition of soil fungi and reduced the biomass of bacteria due to the high content of recalcitrant phenolic compounds (Suseela et al., 2016; Tamura & Tharayil, 2014). Ergosterol was extracted by refluxing 5 g of soil with 10 ml of 0.14 M methanoic-KOH at 80°C in glass tubes lined with Teflon screw caps for 40 min. The supernatant was acidified to a pH < 2 using 0.75 M HCl. The tubes were centrifuged at 2,500 g for 10 min. The supernatant was extracted with 1 ml of hexane at 4°C. The hexane phase was collected into glass vials and dried under N2. The dried content was further reconstituted in 100 µl of 0.1 M KOH in isopropyl alcohol and transferred into glass vials with 250 µl inserts. The amount of ergosterol was quantified using high-pressure liquid chromatography (HPLC). The samples were analysed with a Shimadzu guaternary pump UFLC system equipped with an auto-sampler, inline degasser and UV visible diode array detector. Separation of ergosterol compounds was performed on an Onyx C18 column (monolithic silica, 130°A; 100 mm 4.6 mm I.D.; Phenomenex). The ergosterol was separated by an isocratic elution of 99% methanol. The identification of ergosterol is based on the absorbance of the conjugated double bond at 282 nm. The quantification of ergosterol was based on the comparison of retention time and UV spectra to those of an authentic standard.

2.3.4 | Soil enzyme activity

We measured the potential activity of the hydrolytic enzyme N-acetyl- β -D-glucosaminidase (NAG) that degrades chitin and the oxidative enzyme phenol peroxidase, which helps in the degradation of lignin (Saiya-Cork, Sinsabaugh, & Zak, 2002). See Supporting Information for detailed methods.

2.3.5 | Soil nitrate

Soil nitrate was extracted by shaking 5 g dry soil with 35 ml of 1 M KCl solution for 2 hr on a rotary shaker at 60 rpm. The solution was then centrifuged at 1,050 g for 10 min. The supernatant was filtered through Whatman #1 filter paper and analysed on a flow segmented analyser (Astoria-2; Astoria-Pacific Solution).

2.4 | Statistical analysis

The effect of soil C amendments on plant and soil measurements was analysed using a linear mixed-effects model (LMM) under the restricted maximum likelihood (REML) estimation, with soil C amendments treated as a fixed effect and the block treated as a random effect. The percent cover data were analysed using the above mixed model with soil amendments and species mixture (prairie vs. native) as the fixed factors and block as the random effect. The differences among treatments were compared using post hoc Tukey's HSD multiple comparison test. Statistical tests were considered significant at the p < 0.05 level. All statistical analyses were performed using SAS version 9.4 (SAS Institute, Inc.) and graphs were prepared using Sigmaplot (v14; Systat Software, Inc.).

3 | RESULTS

3.1 | Above-ground biomass and percent cover

In June 2012, the first year after the treatment application, the soils that were amended with activated carbon had higher a percent cover of prairie species (>90%) than both the control and biochar treated plots (Figure 2A). However, during the second year (June 2013), the biochar amended soils had similar percent cover (Figures 2B and 3A,B) and biomass production as that of the activated carbon treated plots (p > 0.05; Figure 4A) and were significantly higher than the control plots (p < 0.001; Figure 4A). The germination percent of native species was very less and hence had significantly lower percent cover in both years compared to that of the prairie species (p < 0.001; Figure 2). During the second year, plots amended with activated



Plant species

FIGURE 2 Percent cover in the carbon amended and the control plots after one year (A) and two years (B) of the application of treatments. Values represent $M \pm SE$ (n = 6) with different lowercase letters indicating difference (Tukey's HSD) among treatments

carbon had the highest biomass production followed by the biochar amended plots (Figure 4A). The control plots had 75% and 66% less biomass compared to the activated carbon and biochar amended plots respectively. In the C amended plots, the emergence of knotweed was lower compared to the control plots (p < 0.001; Figure 4B).

3.2 | Soil fungal biomass (ergosterol)

Soil fungal biomass as indicated by ergosterol was significantly higher in the control plots compared to plots amended with biochar or activated carbon (p = 0.001; Figure 5).

3.3 | Soil enzyme activity

The activity of NAG, an enzyme that catalyses the degradation of chitin from fungal cell walls was higher in control plots compared to that in the activated carbon and biochar amended plots (p < 0.001; Figure 6A).



FIGURE 3 Picture showing the percent cover in the carbon amended and the control plots after two years of treatment application in spring (A) and summer (B). After treatment application, these plots were seeded with prairie seeds



FIGURE 4 Biomass of the prairie species (A) and emergence of knotweed shoots (B) in the carbon amended and the control plots after two years of the application of treatments. Values represent $M \pm SE$ (n = 6) with different lowercase letters indicating difference (Tukey's HSD) among treatments



FIGURE 5 The content of ergosterol in the carbon amended and the control plots after two years of the application of treatments. Values represent $M \pm SE$ (n = 6) with different lowercase letters indicating difference (Tukey's HSD) among treatments



FIGURE 6 The activity of (A) N-acetyl glucosaminidase and (B) phenol peroxidase in the carbon amended and the control plots after two years of the application of treatments. Values represent $M \pm SE$ (n = 5) with different lowercase letters indicating difference (Tukey's HSD) among treatments

However, the trend was opposite in the activity of phenol peroxidase, one of the enzymes that catalyse the degradation of phenolic compounds. The phenol peroxidase activity was markedly lower in control plots compared to the C amended plots (p < 0.01; Figure 6B).



FIGURE 7 The concentration of nitrate in the carbon amended and the control plots after two years of the application of treatments. Values represent $M \pm SE$ (n = 4) with different lowercase letters indicating difference (Tukey's HSD) among treatments

3.4 | Soil nitrate

Soil nitrate also followed the trend of phenol peroxidase activity where the concentration of soil nitrate was five times lower in control plots compared to the activated carbon and biochar amended plots (p = 0.01; Figure 7).

4 | DISCUSSION

The negative impacts of NIPS on invaded habitats may not diminish even after their complete removal (Green et al., 2011; Le Roux et al., 2018; Nsikani et al., 2018), since NIPS can engage in novel niche construction and create a legacy effect through changes in soil C chemistry, nutrient cycling and soil microbial community and functional activity. The influence of soil legacy effect on the continuous suppression of the growth of native species due to the residual allelochemicals from invaders has been widely reported in previous studies (Fisher, Loneragan, & Dixon, 2009; Grove, Haubensak, & Parker, 2012; Kaur, Callaway, & Inderjit, 2014). Although active soil management practices have been demonstrated to be necessary and effective for native plant restoration (Kulmatiski, 2011; Nolan et al., 2015), it remains unclear whether soil C amendments could facilitate native plant restoration in invaded ecosystems through reversing the invader-induced legacy effects. Consistent with this expectation, our results revealed a positive effect of activated carbon and biochar amendments on the percent cover and biomass of prairie species in a Japanese knotweed-invaded ecosystem. More specifically, two years after the application of soil C amendments, soils amended with activated carbon or biochar had 60%-70% more percent cover and biomass of prairie species while had significantly lower emergence of knotweed than the non-amended plots (Figures 2-4). Meanwhile, increased soil N availability and altered microbial activities and fungal biomass in the C amended plots (Figures 5-7) further indicated that C-amendment practices (i.e. activated carbon and biochar) could facilitate the successful reestablishment of the prairie species via reversing the soil legacy effects induced by knotweed invasion.

Introduced, invasive plants can alter soil microbial communities; therefore, native plant restorations could be ultimately considered successful only when the microbial and plant communities are restored to the pre-invasion stages (Pickett, Maltz, & Aronson, 2018). Soil fungal communities play a considerable role in the success of invasive species (Wang et al., 2018; Xiao, Feng, & Schaefer, 2014). In the present study, higher ergosterol (fungal biomass indicator; Figure 5) content was observed in the non-amended soils relative to the soils with C amendments. This result was consistent with the reported fungal-dominated community in the knotweed invaded soils compared to the adjacent non-invaded soils in previous studies from the same site (Suseela et al., 2016; Tamura & Tharayil, 2014). A recent meta-analysis also summarised that the invasion of woody plants increased the biomass of fungi by 77% (Zhang, Li, Wu, & Hu, 2019). The higher fungal biomass in the non-amended soil could be potentially due to the higher abundance of plant secondary metabolites (e.g. phenolic compounds) that remained in the knotweed invaded soil. A higher abundance of monophenolics and flavonoids including tannins was detected in the knotweed-invaded stands from the same site (Suseela et al., 2016; Tharayil et al., 2013). Complex polyphenolic compounds could favour fungi over bacteria in soil since fungi can synthesise oxidoreductase enzymes for the biotic degradation of polyphenols (Winder, Lamarche, Constabel, & Hamelin, 2013). However, the C amended plots had reduced fungal biomass (ergosterol) compared with the control potentially due to the sorption of phenolic compounds by biochar and activated carbon thus lowering the substrate availability to fungi. It has been widely reported that both activated carbon and biochar could alter the soil microbial community composition, and abundance (Domene, Mattana, Hanley, Enders, & Lehmann, 2014; Lehmann et al., 2011). For example, the biochar amendment lowered fungi to bacteria ratio in soils after 12 months of application (Gomez, Denef, & Stewart, 2014). Similarly, the application of activated carbon in invaded stands decreased the fungal abundance by 58% and created a soil microbial condition favouring the growth of native plants (Kulmatiski, 2011). While activated carbon and biochar themselves contain a minor fraction of bioavailable C, which may impact soil micro-organisms (Jones, Haynes, & Phillips, 2010), the high surface area, sorption properties and the shared nature of these two C materials after production make them an ideal surface for the sorption of various aromatic and hydrophobic organic compounds (Bornemann, Kookana, & Welp, 2007; Nolan et al., 2015).

Apart from decreasing the fungal biomass, the C amended plots had altered microbial enzyme activities compared with the control. The potential activity of NAG which degrades chitin from fungal cell walls decreased in the C amended plots consistent with the decrease in fungal biomass in these treatments. However, this trend reversed with phenol peroxidase where the activity of phenol peroxidase was higher in the C amended plots compared with the control. Considering the increased activity of phenol peroxidase in soils treated with both C amendments compared to the non-amended soils (Figure 6A), it is plausible to suggest that one of the most likely explanations for the altered microbial activities after C amendments is the high sorption of phenolic compounds to biochar and activated carbon (Braghiroli, Bouafif, Hamza, Neculita, & Koubaa, 2018; Hall et al., 2014; Michailof, Stavropoulos, & Panaviotou, 2007). The sorption of phenolic compounds made them unavailable to fungi and meanwhile relieved the deactivation of specific microbial enzymes (DeLuca, MacKenzie, Gundale, & Holben, 2006; Suseela et al., 2016). For example, our previous study from the same site indicated that phenol peroxidase activity was negatively affected by flavonoids in knotweed invaded sites (Suseela et al., 2016) and the potential sorption of these phenolic compounds by biochar and activated carbon may have increased the activity of phenol peroxidase. We validated the sorption potential of activated carbon and biochar used in this study using a lab experiment, which revealed that both activated carbon and biochar reduced the concentration of an authentic standard comprised of mixtures of different phenolic compounds (Z. Zhang, unpubl.).

Alteration of soil nutrient availability is considered one of many key factors affecting the invasibility of habitat and the success of invasive species (Dawson, Rohr, van Kleunen, & Fischer, 2012; Zhou & Staver, 2019). Along with the restoration of soil microbial community, effective ecological restoration also requires improved nutrient conditions similar to the pre-invasion level (Roy, Martin, & Irwin, 2010). The nitrate content in C amended soils was five times higher than the non-amended soils indicating that N mineralisation was reduced by knotweed invasion and remained low even two years after completely removing the knotweed, which was consistent with the inhibition of N mineralisation in the same invaded ecosystem in the previous study (Tharayil et al., 2013) and other knotweed invaded sites (Dassonville, Guillaumaud, Piola, Meerts, & Poly, 2011). In contrast to some invaded sites generally featuring higher quantity and quality (e.g. lower C:N and lignin:N ratios) of litter inputs and thus having enhanced soil N cycling (Liao et al., 2008; Sardans et al., 2017; Zhou & Staver, 2019), stands invaded by species (e.g. knotweed in this study) with litter rich in polyphenols such as tannins have been characterised by decreased soil N cycling and lower N availability compared to the native counterparts (Drenovsky & Batten, 2007; Tharayil et al., 2013). In the latter case, higher polyphenols persisted in the invaded soil has been considered the main explanation for the reduced N cycling (Suseela et al., 2016; Tharayil et al., 2013). Polyphenols can complex with proteins and N-containing SOM, slowing N cycling over longer time-scales (Kraus, Dahlgren, & Zasoski, 2003; Madritch & Lindroth, 2015). Polyphenol-protein complexes are resistant to most decomposing organisms, leaving a large portion of N locked within the complexes, which may not be accessible to plants. N mineralisation rates have been demonstrated to decrease substantially with the increasing protein complexing capacity of polyphenols (Hattenschwiler & Vitousek, 2000). The increase in N mineralisation

upon the addition of both soil C amendments could be due to the significant sorption of polyphenols to biochar and activated carbon that made them unavailable. The unavailability of these recalcitrant phenolic compounds by such active interventions may block the protein complexation chain, reactivate microbial enzyme activity and accelerate the conversion of organic N to inorganic forms (Gundale, Sverker, & Albrectsen, 2010; Kraus et al., 2003). Besides altering enzyme-mediated transformation of soil organic N, sorption of phenolic compounds by activated carbon and biochar may reduce the presence of factors inhibitory to nitrification in the soil environment that further allows nitrification to proceed (White, 1994) since phenolics generally have a negative effect on nitrifying bacteria (Berglund, DeLuca, & Zackrisson, 2004; White, 1994). Many studies have reported increased nitrification or abundance of ammonia-oxidising bacteria, a microbial functional group that mediates nitrification, after treatment with both activated carbon and biochar (Ball, MacKenzie, DeLuca, & Montana, 2010; DeLuca et al., 2006; Dempster, Gleeson, Solaiman, Jones, & Murphy, 2012). Although several mechanisms may operate simultaneously to increase the N availability, our study provides direct evidence that soil C amendments (i.e. activated carbon and biochar) could be an effective tool to reverse the invader-created legacy effect on soil N availability and hence the successful growth of non-invasive species. Our study thus emphasises the need to employ active interventions to facilitate the ecological restoration of invaded ecosystems.

Biochar was reported to have a relatively weak sorption capacity compared to activated carbon (Hale, Hanley, & Lehmann, 2011), which is partly evident from the non-significant effect on the percent cover of prairie species one year after treatment application (Figure 2). However, the present results demonstrated that, in year two, both C amendments exhibited similar positive effects on reversing the legacy effect created by knotweed invasion. In addition, from an overall economic and environmental perspective, biochar could be a preferable alternative to activated carbon in restoring invaded ecosystems. Specifically, the large-scale application of activated carbon of invaded lands could become prohibitively expensive, with the cost of using activated carbon in the present study being approximately \$23.36/m². By contrast, the source material and production process for biochar were less expensive (\$0.77/m²). Meanwhile, biochar applied once could be active for longer periods negating the need for repeated application and would be to a lesser extent influenced by soil structure or harsh ageing, compared to activated carbon (Hale et al., 2011). Also, soil amended with biochar could provide additional benefits such as to sequester C, ameliorate soil properties, reduce nutrient leaching and improve soil fertility (Glaser, Lehmann, & Zech, 2002; Lehmann et al., 2011), which might be expected to accelerate the natural recovery of ecosystems in the invaded sites that are resilient to reinvasion. Furthermore, the application of activated carbon could result in an overall negative environmental effect when considering the full life cycle assessment (Arena, Lee, & Clift, 2016). However, caution should be exercised when extending the results of this work to other restoration practices using biochar, as the

outcome of biochar sorption may depend on inherent biochar properties (e.g. pyrolysis temperature), addition rate and plant species (Lehmann et al., 2011). Moreover, as different invaders are characterised with distinct litter chemistry (labile vs. recalcitrant: Tamura & Tharayil, 2014), the effects of these soil C amendments on niche reconstruction and ecological restoration might be context-dependent, which warrants coordinated research networks across a broad range of invaded ecosystems in the future. Also, due to the inherent properties of these C amendments, applying them into the soil will improve soil quality by enhancing porosity, water holding capacity and cation exchange capacity (Atkinson, Fitzgerald, & Hipps, 2010). The effects of these soil amendments on soil structure and functions have been extensively elucidated in many previous studies (Hussain et al., 2017; Kulmatiski, 2011; Lehmann et al., 2011). In our study, the soil was disturbed to a limited extent during the removal of knotweed rhizomes. Alternatively, various chemical and cultural control measures (Jones et al., 2018) could be initially employed to manage knotweed before the application of C amendments as part of the restoration efforts.

5 | CONCLUSIONS

The main focus of our study was to formulate restoration practices that would ameliorate the legacy effect in sites that have been subjected to prolonged invasion by Japanese knotweed. The results of our study support the hypothesis that amending invaded soil with activated carbon and biochar could reverse the niche construction and legacy effect by stimulating soil N mineralisation and altering microbial activities and community structure which promoted the growth of the non-invasive species. The comparison of the efficiency between two soil C amendments employed in this study indicated that biochar could be a more economically feasible alternative to activated carbon in the restoration of invaded ecosystems. Further studies, however, are still required to elucidate the specific mechanisms by which C amendments impact abiotic reactions and microbial transformations that contribute to the reversal of invaderinduced legacy effect. Our findings also emphasise that understanding the mechanisms through which invasive species engage in niche construction is vital in formulating suitable knowledge-based restoration practices for invaded ecosystems.

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AUTHORS' CONTRIBUTIONS

V.S. conceived the idea, conducted the experiment and data analysis; Z.Z. and V.S. wrote the draft of the manuscript; P.C.B. helped with data collection and contributed to writing the manuscript. All authors agreed on the final manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/ 10.5061/dryad.crjdfn327 (Zhang, Bhowmik, & Suseela, 2020).

ORCID

Ziliang Zhang D https://orcid.org/0000-0003-0787-1987 Prasanta C. Bhowmik D https://orcid.org/0000-0002-8172-4208 Vidya Suseela D https://orcid.org/0000-0002-2934-4849

REFERENCES

- Arena, N., Lee, J., & Clift, R. (2016). Life cycle assessment of activated carbon production from coconut shells. *Journal of Cleaner Production*, 125, 68–77. https://doi.org/10.1016/j.jclepro.2016.03.073
- Atkinson, C. J., Fitzgerald, J. D., & Hipps, N. A. (2010). Potential mechanisms for achieving agricultural benefits from biochar application to temperate soils: A review. *Plant and Soil*, 337(1–2), 1–18. https://doi. org/10.1007/s11104-010-0464-5
- Ball, P. N., MacKenzie, M. D., DeLuca, T. H., & Montana, W. E. H. (2010). Wildfire and charcoal enhance nitrification and ammonium-oxidizing bacterial abundance in dry montane forest soils. *Journal of Environmental Quality*, 39, 1243–1253. https://doi.org/10.2134/ jeq2009.0082
- Barney, J. N., Tharayil, N., DiTommaso, A., & Bhowmik, P. C.(2006). The biology of invasive alien plants in Canada. 5. Polygonum cuspidatum Sieb. & Zucc. [= Fallopia japonica (Houtt.) Ronse Decr.]. Canadian Journal of Plant Science, 86(3), 887–906.
- Berglund, L. M., DeLuca, T. H., & Zackrisson, O. (2004). Activated carbon amendments to soil alters nitrification rates in Scots pine forests. *Soil Biology & Biochemistry*, 36, 2067–2073. https://doi.org/10.1016/j. soilbio.2004.06.005
- Blumenthal, D. M., Jordan, N. R., & Svenson, E. L. (2005). Effects of prairie restoration on weed invasions. Agriculture, Ecosystems and Environment, 107, 221–231. https://doi.org/10.1016/j.agee.2004. 11.008
- Bornemann, L. C., Kookana, R. S., & Welp, G. (2007). Differential sorption behaviour of aromatic hydrocarbons on charcoals prepared at different temperatures from grass and wood. *Chemosphere*, 67, 1033– 1042. https://doi.org/10.1016/j.chemosphere.2006.10.052
- Braghiroli, F. L., Bouafif, H., Hamza, N., Neculita, C. M., & Koubaa, A. (2018). Production, characterization, and potential of activated biochar as adsorbent for phenolic compounds from leachates in a lumber industry site. Environmental Science and Pollution Research, 25, 26562–26575. https://doi.org/10.1007/s11356-018-2712-9
- Corbin, J. D., & D'Antonio, C. M. (2012). Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. Invasive Plant Science and Management, 5(1), 117–124. https://doi. org/10.1614/IPSM-D-11-00005.1
- Dassonville, N., Guillaumaud, N., Piola, F., Meerts, P., & Poly, F. (2011). Niche construction by the invasive Asian knotweeds (species complex *Fallopia*): Impact on activity, abundance and community structure of denitrifiers and nitrifiers. *Biological Invasions*, 13, 1115–1133. https://doi.org/10.1007/s10530-011-9954-5
- Dawson, W., Rohr, R. P., van Kleunen, M., & Fischer, M. (2012). Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist*, 194, 859–867. https://doi.org/10.1111/j.1469-8137.2012.04104.x
- DeLuca, T. H., MacKenzie, M. D., Gundale, M. J., & Holben, W. E. (2006). Wildfire-produced charcoal directly influences nitrogen cycling in ponderosa pine forests. *Soil Science Society of America Journal*, 70, 448–453. https://doi.org/10.2136/sssaj2005.0096
- Dempster, D. N., Gleeson, D. B., Solaiman, Z. M., Jones, D. L., & Murphy,
 D. V. (2012). Decreased soil microbial biomass and nitrogen mineralisation with Eucalyptus biochar addition to a coarse textured

soil. Plant and Soil, 354, 311-324. https://doi.org/10.1007/s1110 4-011-1067-5

- Diez, J. M., D'Antonio, C. M., Dukes, J. S., Grosholz, E. D., Olden, J. D., Sorte, C. J. B., ... Miller, L. P. (2012). Will extreme climatic events facilitate biological invasions? *Frontiers in Ecology and the Environment*, 10(5), 249–257. https://doi.org/10.1890/110137
- Domene, X., Mattana, S., Hanley, K., Enders, A., & Lehmann, J. (2014). Medium-term effects of corn biochar addition on soil biota activities and functions in a temperate soil cropped to corn. *Soil Biology & Biochemistry*, 72, 152–162. https://doi.org/10.1016/j.soilbio.2014.01.035
- Drenovsky, R. E., & Batten, K. M. (2007). Invasion by Aegilops triuncialis (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biological Invasions*, 9, 107–116. https://doi.org/10.1007/ s10530-006-0007-4
- Ehrenfeld, J. G. (2003). Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems*, 6(6), 503-523. https://doi. org/10.1007/s10021-002-0151-3
- Elgersma, K. J., Yu, S., Vor, T., & Ehrenfeld, J. G. (2012). Microbialmediated feedbacks of leaf litter on invasive plant growth and interspecific competition. *Plant and Soil*, 356(1–2), 341–355. https://doi. org/10.1007/s11104-011-1117-z
- Evans, R. D., Rimer, R., Sperry, L., & Belnap, J. (2001). Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications*, 11(5), 1301–1310. https://doi.org/10.1890/1051-0761(2001)011[1301:E-PIAND]2.0.CO;2
- Farrer, E. C., & Goldberg, D. E. (2009). Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications*, 19(2), 398–412. https://doi.org/10.1890/08-0485.1
- Fisher, J. L., Loneragan, W. A., Dixon, K., & Veneklaas, E. (2009). Soil seed bank compositional change constrains biodiversity in an invaded species-rich woodland. *Biological Conservation*, 142, 256–269.
- Gessner, M. O., & Schmitt, A. L. (1996). Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. Applied and Environmental Microbiology, 62(2), 415–419.
- Glaser, B., Lehmann, J., & Zech, W. (2002). Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal – A review. *Biology and Fertility of Soils*, 35, 219–230.
- Glass, S. (2004). Ecological restoration as a strategic framework for invasive species management planning: The University of Wisconsin experience. Proceedings of the North American Prairie Conferences. 84.
- Gomez, J. D., Denef, K., Stewart, C. E., Zheng, J., & Cotrufo, M. F. (2014). Biochar addition rate influences soil microbial abundance and activity in temperate soils. *European Journal of Soil Science*, 65, 28–39.
- Green, P. T., O'Dowd, D. J., Abbott, K. L., Jeffery, M., Retallick, K., & Mac Nally, R. (2011). Invasional meltdown: Invader-invader mutualism facilitates a secondary invasion. *Ecology*, 92, 1758–1768.
- Grove, S., Haubensak, K. A., & Parker, I. M. (2012). Direct and indirect effects of allelopathy in the soil legacy of an exotic plant invasion. *Plant Ecology*, 213(12), 1869–1882.
- Gundale, M. J., Sverker, J., Albrectsen, B. R., Nilsson, M.-C., & Wardle, D. (2010). Variation in protein complexation capacity among and within six plant species across a boreal forest chronosequence. *Plant Ecology*, 211, 253–266.
- Hale, S., Hanley, K., Lehmann, J., Zimmerman, A. R., & Cornelissen, G. (2011). Effects of chemical, biological, and physical aging as well as soil addition on the sorption of pyrene to activated carbon and biochar. Environmental Science & Technology, 45(24), 10445–10453.
- Hall, K. E., Calderon, M. J., Spokas, K. A., Cox, L., Koskinen, W. C., Novak, J., & Cantrell, K. (2014). Phenolic acid sorption to biochars from mixtures of feedstock materials. *Water, Air, & Soil Pollution, 225, 2031.* https://doi.org/10.1007/s11270-014-2031-9
- Hattenschwiler, S., & Vitousek, P. M. (2000). The role of polyphenols in terrestrial ecosystem nutrient cycling. *Trends in Ecology & Evolution*, 15, 238–243. https://doi.org/10.1016/S0169-5347(00)01861-9

- Hussain, M., Farooq, M., Nawaz, A., Al-Sadi, A. M., Solaiman, Z. M., Alghamdi, S. S., ... Siddique, K. H. M. (2017). Biochar for crop production: Potential benefits and risks. *Journal of Soil Sediments*, 17, 685–761. https://doi.org/10.1007/s11368-016-1360-2
- Jones, D., Bruce, G., Fowler, M. S., Law-Cooper, R., Graham, I., Abel, A., ... Eastwood, D. (2018). Optimising physiochemical control of invasive Japanese knotweed. *Biological Invasions*, 20(8), 2091–2105.
- Jones, B. E. H., Haynes, R. J., & Phillips, I. R. (2010). Effect of amendment of bauxite processing sand with organic materials on its chemical, physical and microbial properties. *Journal of Environmental Management*, 91, 2281–2288. https://doi.org/10.1016/j.jenvm an.2010.06.013
- Kaur, R., Callaway, R. M., & Inderjit . (2014). Soils and the conditional allelopathic effects of a tropical invader. *Soil Biology & Biochemistry*, 78, 316–325. https://doi.org/10.1016/j.soilbio.2014.08.017
- Kraus, T. E. C., Dahlgren, R. A., & Zasoski, R. J. (2003). Tannins in nutrient dynamics of forest ecosystems – A review. *Plant and Soil*, 256, 41–66. https://doi.org/10.1023/A:1026206511084
- Kulmatiski, A. (2011). Changing soils to manage plant communities: Activated carbon as a restoration tool in ex-arable fields. *Restoration Ecology*, 19, 102–110. https://doi.org/10.1111/j.1526-100X.2009.00632.x
- Kulmatiski, A., Beard, K. H., & Stark, J. M. (2006). Soil history as a primary control on plant invasion in abandoned agricultural fields. *Journal of Applied Ecology*, 43(5), 868–876. https://doi. org/10.1111/j.1365-2664.2006.01192.x
- Larson, D. L., Bright, J. B., Drobney, P., Larson, J. L., Palaia, N., Rabie, P. A., ... Wells, D. (2013). Using prairie restoration to curtail invasion of Canada thistle: The importance of limiting similarity and seed mix richness. *Biological Invasions*, 15, 2049–2063. https://doi. org/10.1007/s10530-013-0432-0
- Lattanzio, V., Kroon, P. A., Quideau, S., & Treutter, D. (2008). Plant phenolics—Secondary metabolites with diverse functions. *Recent Advances in Polyphenol Research*, 1, 1–35.
- Le Roux, J. J., Ellis, A. G., van Zyl, L.-M., Hosking, N. D., Keet, J.-H., & Yannelli, F. A. (2018). Importance of soil legacy effects and successful mutualistic interactions during Australian acacia invasions in nutrient-poor environments. *Journal of Ecology*, 106, 2071–2081. https:// doi.org/10.1111/1365-2745.12965
- Lehmann, J., Rillig, M. C., Thies, J., Masiello, C. A., Hockaday, W. C., & Crowley, D. (2011). Biochar effects on soil biota – A review. Soil Biology & Biochemistry, 43, 1812–1836. https://doi.org/10.1016/j. soilbio.2011.04.022
- Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., ... Li, B. O. (2008). Altered ecosystem carbon and nitrogen cycles by plant invasion: A meta-analysis. *New Phytologist*, 177, 706–714. https://doi. org/10.1111/j.1469-8137.2007.02290.x
- Madritch, M. D., & Lindroth, R. L. (2015). Condensed tannins increase nitrogen recovery by trees following insect defoliation. New Phytologist, 208, 410–420. https://doi.org/10.1111/nph.13444
- Malcolm, G. M., Bush, D. S., & Rice, S. K. (2008). Soil nitrogen conditions approach preinvasion levels following restoration of nitrogenfixing Black Locust (*Robinia pseudoacacia*) stands in a pine-oak ecosystem. *Restoration Ecology*, 16(1), 70-78. https://doi.org/10. 1111/j.1526-100X.2007.00263.x
- Maurel, N., Salmon, S., Ponge, J.-F., Machon, N., Moret, J., & Muratet, A. (2010). Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions*, 12(6), 1709–1719. https://doi.org/10.1007/s10530-009-9583-4
- Michailof, C., Stavropoulos, G. G., & Panayiotou, C. (2007). Enhanced adsorption of phenolic compounds, commonly encountered in olive mill wastewaters, on olive husk derived activated carbons. *Bioresource Technology*, 99(14), 6400–6408. https://doi.org/10.1016/j.biortech.2007.11.057
- Miki, T. (2012). Microbe-mediated plant-soil feedback and its roles in a changing world. *Ecological Research*, 27(3), 509–520. https://doi. org/10.1007/s11284-012-0937-5

- Miki, T., & Kondoh, M. (2002). Feedbacks between nutrient cycling and vegetation predict plant species coexistence and invasion. *Ecology Letters*, 5(5), 624–633. https://doi.org/10.1046/j.1461-0248.2002.00347.x
- Nolan, N. E., Kulmatiski, A., Beard, K. H., & Norton, J. M. (2015). Activated carbon decreases invasive plant growth by mediating plant-microbe interactions. *AoB Plants*, 7. https://doi.org/10.1093/aobpla/plu072
- Northup, R. R., Yu, Z., Dahlgren, R. A., & Vogt, K. A. (1995). Polyphenol control of nitrogen release from pine litter. *Nature*, 377(6546), 227. https://doi.org/10.1038/377227a0
- Nsikani, M. M., van Wilgen, B. W., & Gaertner, M. (2018). Barriers to ecosystem restoration presented by soil legacy effects of invasive alien N₂-fixing woody species: Implications for ecological restoration. *Restoration Ecology*, 26, 235–244.
- Pickett, B., Maltz, M., & Aronson, E. (2018). Impacts of invasive plants on soil fungi and implications for restoration. In S. C. Sahu, & S. Kumar (Eds.), *Invasive species* (pp. 45–62). IntechOpen.
- Pringle, A., Bever, J. D., Gardes, M., Parrent, J. L., Rillig, M. C., & Klironomos, J. N. (2009). Mycorrhizal symbioses and plant invasions. Annual Review of Ecology, Evolution, and Systematics, 40, 699–715. https://doi.org/10.1146/annurev.ecolsys.39.110707.173454
- Reinhart, K. O., & Callaway, R. M. (2006). Soil biota and invasive plants. New Phytologist, 170(3), 445–457. https://doi. org/10.1111/j.1469-8137.2006.01715.x
- Roy, E. D., Martin, J. F., Irwin, E. G., Conroy, J. D., & Culver, D. A. (2010). Transient social-ecological stability: The effects of invasive species and ecosystem restoration on nutrient management compromise in Lake Erie. *Ecology and Society*, 15, 20.
- Saiya-Cork, K. R., Sinsabaugh, R. L., & Zak, D. R. (2002). The effects of long term nitrogen deposition on extracellular enzyme activity in an Acer saccharum forest soil. Soil Biology & Biochemistry, 34(9), 1309– 1315. https://doi.org/10.1016/S0038-0717(02)00074-3
- Sardans, J., Bartrons, M., Margalef, O., Gargallo-Garriga, A., Janssens, I. A., Ciais, P., ... Peñuelas, J. (2017). Plant invasion is associated with higher plant-soil nutrient concentrations in nutrient-poor environments. *Global Change Biology*, 23, 1282–1291. https://doi. org/10.1111/gcb.13384
- Sorte, C. J. B., Ibáñez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., ... Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, 16(2), 261–270. https://doi. org/10.1111/ele.12017
- Suseela, V., Alpert, P., Nakatsu, C. H., Armstrong, A., & Tharayil, N. (2016). Plant-soil interactions regulate the identity of soil carbon in invaded ecosystems: Implication for legacy effects. *Functional Ecology*, 30, 1227–1238. https://doi.org/10.1111/1365-2435.12591
- Suseela, V., & Tharayil, N. (2018). Decoupling the direct and indirect effects of climate on plant litter decomposition: Accounting for stress-induced modifications in plant chemistry. *Global Change Biology*, 24(4), 1428–1451. https://doi.org/10.1111/gcb.13923
- Tamura, M., Suseela, V., Simpson, M., Powell, B., & Tharayil, N. (2017). Plant litter chemistry alters the content and composition of organic carbon associated with soil mineral and aggregate fractions

in invaded ecosystems. *Global Change Biology*, 23(10), 4002–4018. https://doi.org/10.1111/gcb.13751

- Tamura, M., & Tharayil, N. (2014). Plant litter chemistry and microbial priming regulate the accrual, composition and stability of soil carbon in invaded ecosystems. *New Phytologist*, 203, 110–124. https://doi. org/10.1111/nph.12795
- Tharayil, N., Alpert, P., Bhowmik, P., & Gerard, P. (2013). Phenolic inputs by invasive species could impart seasonal variations in nitrogen pools in the introduced soils: A case study with *Polygonum cuspidatum*. *Soil Biology & Biochemistry*, *57*, 858–867. https://doi.org/10.1016/j.soilb io.2012.09.016
- Von Holle, B., & Simberloff, D. (2004). Testing Fox's assembly rule: Does plant invasion depend on recipient community structure? Oikos, 105(3),551–563. https://doi.org/10.1111/j.0030-1299.2004.12597.x
- Wang, C., Zhou, J., Liu, J., Jiang, K., Xiao, H., & Du, D. (2018). Responses of the soil fungal communities to the co-invasion of two invasive species with different cover classes. *Plant Biology*, 20, 151–159. https:// doi.org/10.1111/plb.12646
- White, C. S. (1994). Monoterpenes Their effects on ecosystem nutrient cycling. *Journal of Chemical Ecology*, 20, 1381–1406. https://doi. org/10.1007/BF02059813
- Winder, R. S., Lamarche, J., Constabel, C. P., & Hamelin, R. C. (2013). The effects of high-tannin leaf litter from transgenic poplars on microbial communities in microcosm soils. *Frontiers in Microbiology*, 4, e290. https://doi.org/10.3389/fmicb.2013.00290
- Xiao, H. F., Feng, Y. L., Schaefer, D. A., Dong Yang, X. (2014). Soil fungi rather than bacteria were modified by invasive plants, and that benefited invasive plant growth. *Plant and Soil*, 378, 253–264.
- Zhang, P., Li, B. O., Wu, J., & Hu, S. (2019). Invasive plants differentially affect soil biota through litter and rhizosphere pathways: A meta-analysis. *Ecology Letters*, 22, 200–210. https://doi.org/10.1111/ ele.13181
- Zhang, Z., Bhowmik, P. C., & Suseela, V. (2020). Data from: Effect of soil carbon amendments in reversing the legacy effect of plant invasion. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.crjdfn327
- Zhou, Y., & Staver, A. C. (2019). Enhanced activity of soil nutrient-releasing enzymes after plant invasion: A meta-analysis. *Ecology*, 100(11), e2830. https://doi.org/10.1002/ecy.2830

SUPPORTING INFORMATION

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