Plant Soil (2023) 484:65–77
https://doi.org/10.1007/s11104-022-05739-0

RESEARCH ARTICLE

# Solidago canadensis invasion destabilizes the understory plant community and soil properties of coastal shelterbelt forests of subtropical China

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Received: 15 May 2022 / Accepted: 5 October 2022 / Published online: 15 October 2022


**Abstract**
*Aims* Canadian goldenrod (*Solidago canadensis*) invasion is degrading the coastal shelterbelt forests of subtropical China, but few studies have quantified the role of this invader in structuring understory plant diversity and soil properties.
*Methods* Understory species richness, Margalef index, Pielow index, community stability index, soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), C:N ratio, pH, bulk porosity (BP), and aeration porosity (AP) were assessed by deriving three categories of goldenrod invasion in coastal shelterbelt forests of Zhejiang, China, that is, uninvaded, moderately invaded and severely invaded plant communities according to goldenrod coverage.
*Results* Goldenrod invasion was generally associated with significantly decreased understory plant richness and community stability, but increased species evenness. Specifically, moderate invasion was associated with substantially fewer species compared to uninvaded communities, it was also associated with increased SOC, C:N ratio, CEC, and AP but decreased TN. However, severe invasion was only associated with slight additional declines in species richness compared to moderate invasion, but further reduced soil TN, SOC, and CEC. Soil TN and TP were both strongly and positively associated with community stability and understory plant species richness. However, severe invasion decoupled the correlational relationships between soil TN and understory community stability.
*Conclusions* Moderate invasion of goldenrod caused reduced plant taxonomic diversity and altered soil nutrients in coastal shelterbelt forests of

Responsible Editor: François Teste.

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**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11104-022-05739-0.

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subtropical China. Severe invasion aggravated the impacts a step further, and decoupled soil TN and understory community stability. These results illuminate the impacts of goldenrod invasion on community structure and soil properties in coastal shelterbelt forests and provide evidence that invasive plants can significantly alter the ecological processes in introduced communities.

**Keywords** Goldenrod invasion · Coastal shelterbelt forests · Understory plant diversity · Soil properties · Community stability

## Introduction

Biological invasions are one of the main threats to biological conservation and ecosystem function, especially when increasing globalization accelerates the introduction of alien invasive plants to new ecological communities (van Kleunen et al. 2015; Seebens et al. 2017). Plant invasions can cause large shifts in local soil conditions, alter community composition and structure, and impact ecosystem services by affecting community stability and functionality (Shearer et al. 2007). Plant invasions have been reported to directly decrease species abundance and affect soil nutrient uptake and hydrologic cycling in the United States (Pimentel et al. 2005; Yelenik and D'Antonio 2013). In forested ecosystems, plant invasions reduce timber production and biomass accumulation by limiting desired reproduction and growth and decreasing the provisioning of important non-market goods and services in several northern hemisphere countries (e.g., China, USA, Russia) (Liebhold et al. 2017).

Canadian goldenrod (*Solidago canadensis* L., 'goldenrod' hereafter) is an herbaceous species native to northeastern and north-central North America, but it can be considered an invasive species in ranges including large parts of Asia, Europe, Australia, and New Zealand (Lu et al. 2007). It was officially recognized as an invasive plant in 2010 by China (Long et al. 2015). Goldenrod has characteristics typical of other invasive herbaceous plants, such as rapid growth and spread, high fecundity, clonality, and allelochemicals, which exclude the establishment of other plants (Dong et al. 2006; Abhilasha et al. 2008; Zhang et al. 2009b). Invasion by goldenrod has been reported in various ecological communities in China, with invasions most often occurring in urban areas, agricultural systems, and abandoned fields (Schittko and Wurst 2014; Wang et al. 2018). It is now a widely distributed invasive plant in eastern China and in some regions, it forms extensive, highly homogenous plant populations (Guo et al. 2010; Wang et al. 2019). A variety of studies have documented the biological, physiological, and ecological characteristics of goldenrod, but the ecological responses vary depending on the ecosystem (Nolf et al. 2014; Immel et al. 2012; Liao et al. 2011). In urban areas, disturbance and land use impacts from urbanization facilitate the invasion of goldenrod. While in coastal shelterbelt forest communities, soil nutrients and alterations to soil properties may have a more profound influence on invasion dynamics due to the distinctive traits of nutrient deficits in reclaimed sea lands (Pyšek et al. 2012; Xie et al. 2021). However, few studies have evaluated the effects of goldenrod invasion on community structure, composition, and function of coastal shelterbelt forests, despite that these built communities are ecologically and economically important to China (An et al. 2006).

Coastal shelterbelt forests in China are generally afforested lands reclaimed from the sea with substantial human and economic investments (Fig. S1). These forests play an incredibly important role in improving soil nutrients, greening suburban landscapes, sheltering from sea breeze, sequestering carbon, and mitigating impacts from storms and typhoons (An et al. 2006; Wang et al. 2013). But the harsh natural environments and infertile soils in these areas allow few natural plant communities to exist prior to tree establishment (Xie et al. 2018). Tree species used for afforestation have strong resistance to salinity, including species such as *Casuarina equisetifolia*, *Robinia pseudoacacacia,* and *Populus nigra*. However, species also vary between ecoregions and more than hundred tree species have been suggested or utilized for coastal shelterbelt afforestation [China: National Coastal Shelter Forest System Construction Project Planning (2016–2025)]. The primary criteria for tree species selection is survival and growth, despite that some of the selected species are non-native. Surviving trees may subsequently form a relatively stable community. But external disturbances, like goldenrod invasion, has led to evident degradation of the coastal shelterbelts in eastern China, including Shanghai, Zhejiang, and Jiangsu province. Goldenrod invasion in these forests has resulted in tree death and the discontinuity of shelterbelts (Wang et al. 2021). Goldenrod is also a great consumer of available resources resulting in overwhelming competitive advantages over some originally established understory plants, thus invasion may reduce coastal shelterbelt forest community stability and ecosystem functionality (Hu et al. 2022).

Soil physiochemical properties are considered one of the major abiotic factors influencing community succession in systems invaded by invasive plants (Zhang et al. 2009a). Compared with native plants, invasive plants typically exhibit higher nutrient uptake efficiencies and may subsequently decrease available soil nutrients available for other plants (Osborne and Gioria 2018). Especially in nutrient-limited ecosystems, competition by invasive plants could reduce the overall plant diversity and community stability (Zhou and Staver 2019). Invasive plants also alter soil nutrients through large inputs of leaf litter, differences in root distribution, interactions with microorganisms, and allelopathic compounds affecting belowground nutrient cycling and functioning (Chávez-Vergara et al. 2015; Allen et al. 2015). Thus, the relationship between understory plant diversity and soil physiochemical properties becomes a key factor for the restoration of invader-induced degradation of coastal shelterbelt forests (Xie et al. 2018).

From prior studies, we found that coastal shelterbelt forests in Eastern China that are dominated by Chinese flame tree (*Koelreuteria bipinnata* Franch.) are being widely invaded by goldenrod, and on some sites, the invasion is quite severe. On sites with severe goldenrod invasions, it was observed that the structure and composition of understory plants had been dramatically altered, and the coastal shelterbelts degraded noticeably. This study was designed to evaluate the effects of goldenrod invasion severity on coastal shelterbelt forests, we want to assess differences in understory plant taxonomic diversity, community stability, and soil physiochemical properties associated with goldenrod dominance. We specifically evaluated three goldenrod invasion severities (i.e., uninvaded, moderately invaded, and severely invaded) categorized according to goldenrod coverage.

We hypothesized that: 1) the severity of goldenrod invasion is negatively associated with understory plant richness, as increases in invasive plant abundance are often related to decreases in native plant diversity; 2) goldenrod invasion would increase soil porosity and decrease chemical nutrients in comparison to less invaded or uninvaded sites, because invasive plants often have massive root systems and higher nutrient uptake efficiencies; and 3) soil N is an important determinant affecting understory plant community characteristics, but severe goldenrod invasion will reduce the association between soil N and understory community stability observed in uninvaded communities.

## Material and methods

### Study area

Three independent sites in Zhejiang province (Haining city, Xiangshan county and Taizhou city) were selected for the study (Fig. 1). The sites range from 3.5 to 4.5 m above mean sea level, with an average of 1187 to 1632 mm of precipitation per year and occupy similar soil orders (Table 1). These sites all had 17 ~ 20 years old coastal shelterbelt forests developed through afforestation practices using predominately Chinese flame tree, occupying 70%-75% of the overstory. Other associated tree species include Chinese sweetgum (*Liquidambar formosana*) and wax-leaf privet (*Ligustrum compactum*), representing about 25%-30% of the overstory. The understory plants were regenerated naturally with little manipulation or management since the afforestation was finished. Presently, dominant understory herbaceous plants include *Setaria viridis*, *Brassica juncea*, *Paederia scandens*, *Agropyron cristatum*, *Euphorbia lathyrism*, *Pharbitis nil*, and *Solanum nigrum.* Although some of the species are non-native, they are not considered invasive to the shelterbelt ecosystem. Shrubs are not a component of these sites. According to the local forestry administration records, all three sites had goldenrod present for at least four years prior to our study and represented similar environmental conditions (i.e., major weather-related disturbances).

### Experimental design and sampling

In September 2017, we randomly set up 93 plots (2 m × 2 m) within the three coastal shelterbelt forest sites to investigate goldenrod invasion,

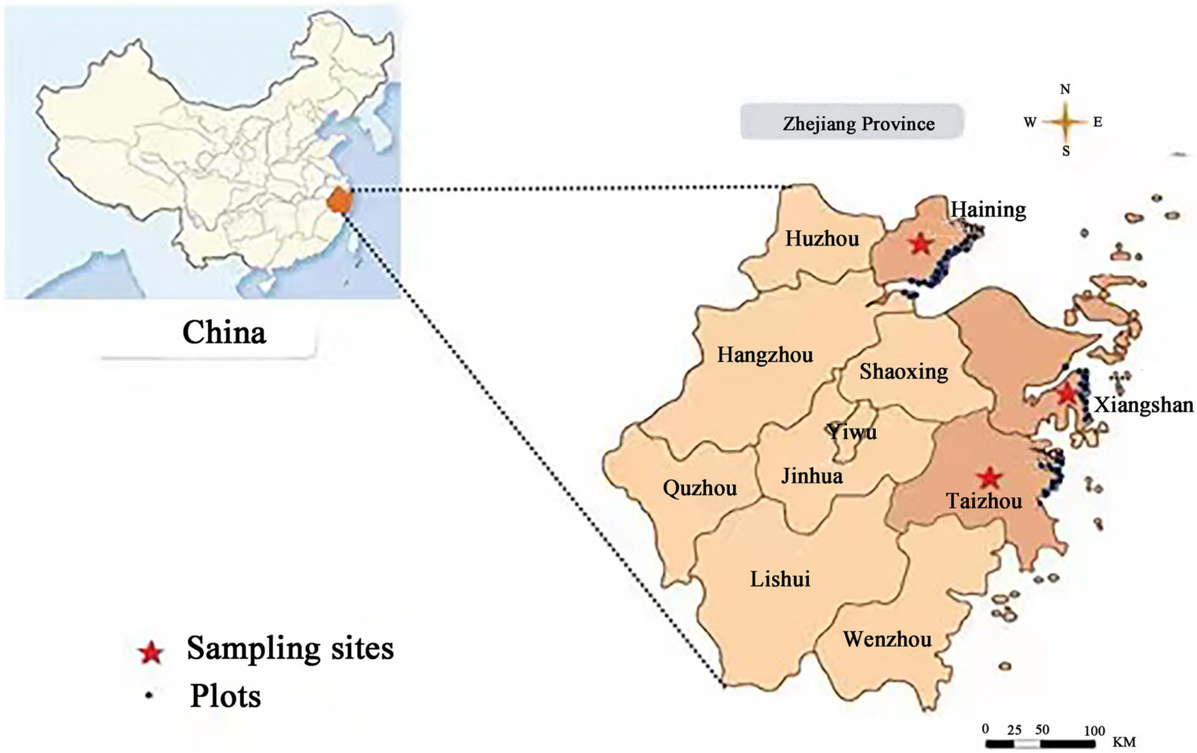


**Fig. 1** Experimental study area and sampling sites

**Table 1** Site characteristics of the experimental areas

| Site characteristics | Experimental sites | | |
|---|---|---|---|
| | Haining | Xiangshan | Taizhou |
| Longitude (°) | 120.82 | 121.94 | 121.60 |
| Latitude (°) | 30.30 | 29.39 | 28.55 |
| Altitude (m) | 4.5 | 3.5 | 4.0 |
| Mean Annual temperature (°C) | 15.9 | 16.5 | 16.9 |
| Mean Annual rainfall (mm) | 1187 | 1415 | 1632 |
| Soil order | Ultisols | Ultisols | Ultisols |

including 39 plots in Haining City, 27 plots in Xiangshan County, and 27 plots in Taizhou City. When plots were established, we considered the influence of tree age, species composition, density, canopy coverage, soil properties and climate to ensure "invasion severity" as the main attributable variable affecting understory plant composition and soil. In all plots, goldenrod was the only invasive species present. Three goldenrod invasion severity categories were established according to the soil coverage of goldenrod in the plot, resulting in the following classifications: UI (uninvaded, goldenrod absent), MI (moderately invaded, goldenrod coverages ranging from trace coverage to 40%), and SI (severely invaded, goldenrod coverages greater than 40%). Goldenrod coverage equals to the soil cover percentage of goldenrod in each plot and was estimated visually. To improve accuracy, each plot was divided into 4 subplots (1 m × 1 m) to estimate the goldenrod coverage separately, then the subplots were summed to calculate the total plot goldenrod coverage. The reason we selected 40% goldenrod coverage as the minimum threshold for severe invasion was based on the observation that the majority native understory plants were excluded from plots at this level. In each plot, we recorded plant species, the number of individuals per species, and the total number of individuals (Table S2).

Soil samples were taken in each plot. Soil samples for chemical analysis were obtained with stainless soil augers (5 cm in diameter), collecting soil mixtures of 0–20 cm from 5 points (the four plot corners and a center point) and thoroughly mixed to obtain a composite sample for each plot. These soil samples were air-dried at room temperature and sieved through a 3-mm mesh screen to remove visible plant debris and stones in preparation for analysis. Soil samples for physical analysis were obtained with the ring-knife method, collecting three samples (two random plot corners and a center point) for each plot; samples were kept in their original shapes and transported to the laboratory. Soil organic carbon (SOC) was measured using the potassium dichromate oxidation-external heating method. Soil total nitrogen (N) was estimated with perchloric acid-sulfuric acid digestion diffusion absorption, and soil total phosphorous (P) was analyzed with perchloric acid-sulfuric acid-soluble Mo-Sb colorimetry. Soil pH was measured based on air-dried and 2-mm sieved subsamples using a pH electrode placed in a fresh volume ratio of 1:2 in 0.01 M $CaCl_2$. Soil cation exchange capacity (CEC) was determined using the ammonium chloride sodium acetate ($NH_4Cl$-$NH_4OAc$) method (Hu et al. 2021). Soil bulk porosity (BP) and aeration porosity (AP) were measured with the ring-knife method (Bao 2007).

## Indices measurement

Species richness, Margalef index, Pielow index, and community stability index were calculated with Eq. (1, 2, 3 and 4) to characterize the understory plant diversity. For each diversity index, we used absolute numbers (total number of individuals of each species in each plot) for calculation. Margalef index is an easily applied index for species richness while accounting for sampling effects (Gamito 2010). Pielow index is a measure of species evenness (Smith and Wilson 1996). We used community stability index to assess plant communities with the severity of invasion rather than assessing invasion impacts through time with repeated measures. Our approach differs from Valone and Balaban-Feld's temporal stability (2018), as we assessed differences in plant communities at different invasion levels allowing for comparisons between our study plots (Wang et al. 2019). Soil SOC, total N, total P, C:N ratio, pH, CEC, BP and AP were used to assess soil physiochemical properties, which are all important parameters associated with soil nutrient availability and can be used to characterize, to a certain extent, alterations to the soil nutrients and cycling environment.

$$\text{Species richness} = \mathrm{S} \tag{1}$$

$$\text{Margalef index (D)} = (\mathrm{S} - 1)/\ln \mathrm{N} \tag{2}$$

$$\text{Pielou index (J)} = \mathrm{H}'/\ln \mathrm{S} \tag{3}$$

$$\text{Community stability index} = \mu/\sigma \tag{4}$$

where S is the total number of species, H′ is Shannon–Wiener index, N is the total number of individuals in the plot. $\mu$ is the average value of relative abundance of all plant species in a particular plot, $\sigma$ is the standard deviation for the average value of relative abundance of all plant species in a plot.

## Data analysis

Data normality and homogeneity were evaluated before performing the subsequent statistical analyses. If data were non-normal, they were log-transformed or square root-transformed to improve normality and reduce heteroscedasticity. Data are reported as mean ± SD for understory plant diversity indices and soil property indicators among the goldenrod invasion severities. Linear mixed models were used to compare understory species diversity and soil properties with invasion severity as a fixed effect and site as a random factor, tree age and canopy coverage were included in the models as covariates. If a significant effect was detected ($p < 0.05$), post hoc pairwise comparisons followed to estimate the differences among the invasion severities. Two-way ANOVAs were used to model the effects of invasion severity, site, and their interactions on soil properties. Redundancy analysis (RDA) was performed using Canoco 5.0 (Lai 2013). The relationships between understory plant diversity and soil properties were evaluated with correlational analyses. Statistical analyses were conducted using SPSS 20.0 (IBM, USA) and Origin 2020 Pro (OriginLab, USA), with significance levels set at $P < 0.05$.

## Results

### Association of invasion severity with understory plant diversity

Of the 93 plots, 36 were classified as UI, 30 as MI, and 27 as SI (Table S1). The average total coverage of goldenrod in MI and SI plots are 26.4% ± 4.8% and 47.5% ± 6.9% (data are mean ± SD), respectively. Among plots, plant community diversity differed according to severity of goldenrod invasion. Specifically, understory plant richness, Margalef index, and community stability index were lower on sites with any level of goldenrod invasion (Fig. 2A, B, D). Species richness is greater in UI, followed by MI, and is the lowest in SI. Moderate invasion greatly reduced species richness while severe invasion only reduced slightly from MI. In Haining and Xiangshan, increased plot evenness was positively associated with invasion severity. However, in Taizhou City, evenness did not differ regardless of invasion status (Fig. 2C) ($P < 0.05$). In Haining and Taizhou, severe invasion did not significantly affect community stability when compared to moderately invaded plots, but a decreasing trend was observed. However, in Xiangshan, severe invasion further reduced community stability (Fig. 2D) ($P < 0.05$).

### Association of invasion severity with soil physiochemical properties

Invasion severity, site, and their interactions all had significant effects on SOC, TP, C: N ratio, and BP. Invasion severity alone had significant effects on all the parameters except pH, while site differences had no significant effects on pH or CEC. The interaction of invasion severity and site differences had extremely significant effects on all the involved parameters (Table 2).

Goldenrod invasion was significantly correlated to changes in soil nutrients. Specifically, across all

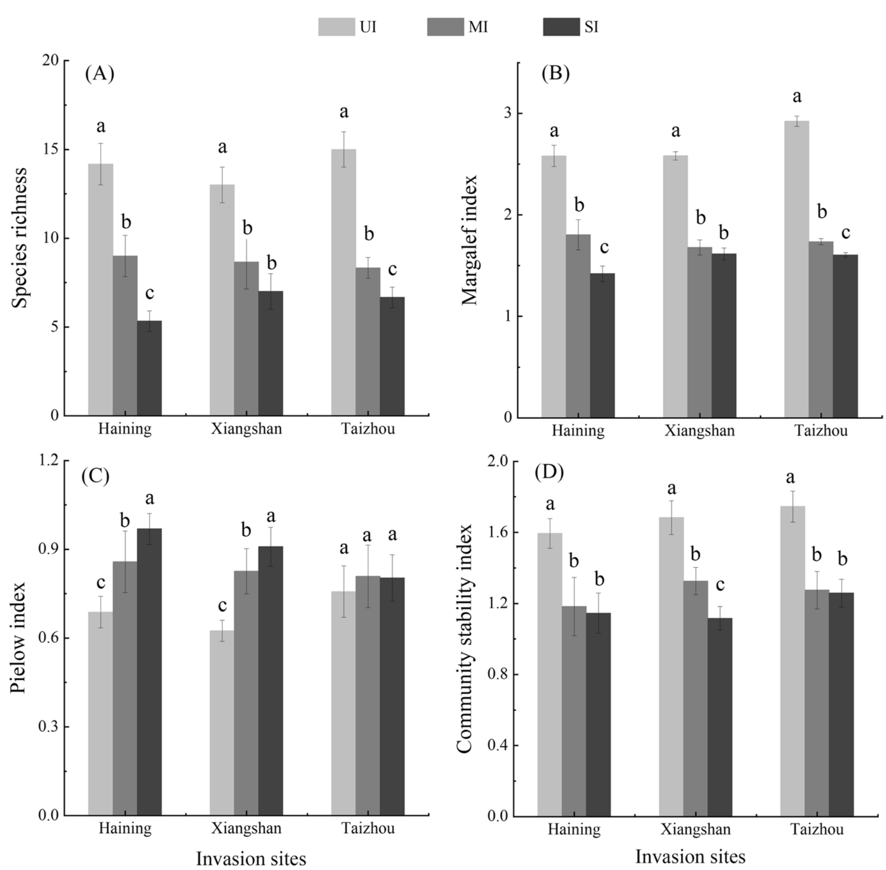


**Fig. 2** Association of goldenrod invasion severity with understory plant diversity in coastal shelterbelt forests. UI means uninvaded, MI means moderately invaded, SI means severely invaded. Different letters within the same sites indicate significant differences between species richness, Margalef index, Pielow index, and community stability index among invasion severities ($P < 0.05$), ($N_{UI} = 36$, $N_{MI} = 30$, $N_{SI} = 27$)

**Table 2** Two-way ANOVA comparing effects of invasion severity and site on soil physiochemical properties

| Factor | *DF* | SOC | TN | TP | C: N ratio | pH | CEC | BP | AP |
|---|---|---|---|---|---|---|---|---|---|
| Severity | 2 | 32.183** | 89.284** | 46.440** | 55.106** | 0.668 | 25.950** | 13.556** | 184.599** |
| Site | 2 | 6.158** | 5.314* | 7.123** | 9.909** | 0.394 | 0.497 | 7.962** | 4.893* |
| Severity × Site | 4 | 10.963** | 9.296** | 9.763** | 10.038** | 5.049** | 6.974** | 5.728** | 9.749** |

** indicates significant level at $P<0.01$, * indicates significant level at $P<0.05$. *SOC* soil organic carbon; *TN* total nitrogen, *TP* total phosphorus, *C: N ratio* carbon: nitrogen ratio, *CEC* cation exchange capacity, *BP* bulk porosity, *AP* aeration porosity

three sites, moderate invasion was associated with increased SOC and C:N ratio but decreased total N. Moderate invasion was also associated with decreased total P in Xiangshan and Taizhou, while there was no effect in Haining. Further, at all three sites, severe invasion reduced SOC and total N, while total P was reduced in Xiangshan and Taizhou only. Severe invasion was associated with an elevated C:N ratio in Xiangshan and Taizhou. However, for Haining, C:N ratio was greatest for moderately invaded plots when compared to severely or uninvaded plots (Fig. 3).

Soil CEC was remarkably higher in moderately invaded plots but lower in those severely invaded (Fig. 4B). Goldenrod invasion generally enhanced bulk porosity and aeration porosity but there were notable site differences (Fig. 4B, C). No relationship was detected for soil pH among the invasion severities in Haining and Xiangshan, but there were differences in Taizhou, in which both moderate and severe invasions significantly increased soil pH compared to the uninvaded plots. (Fig. 4A).

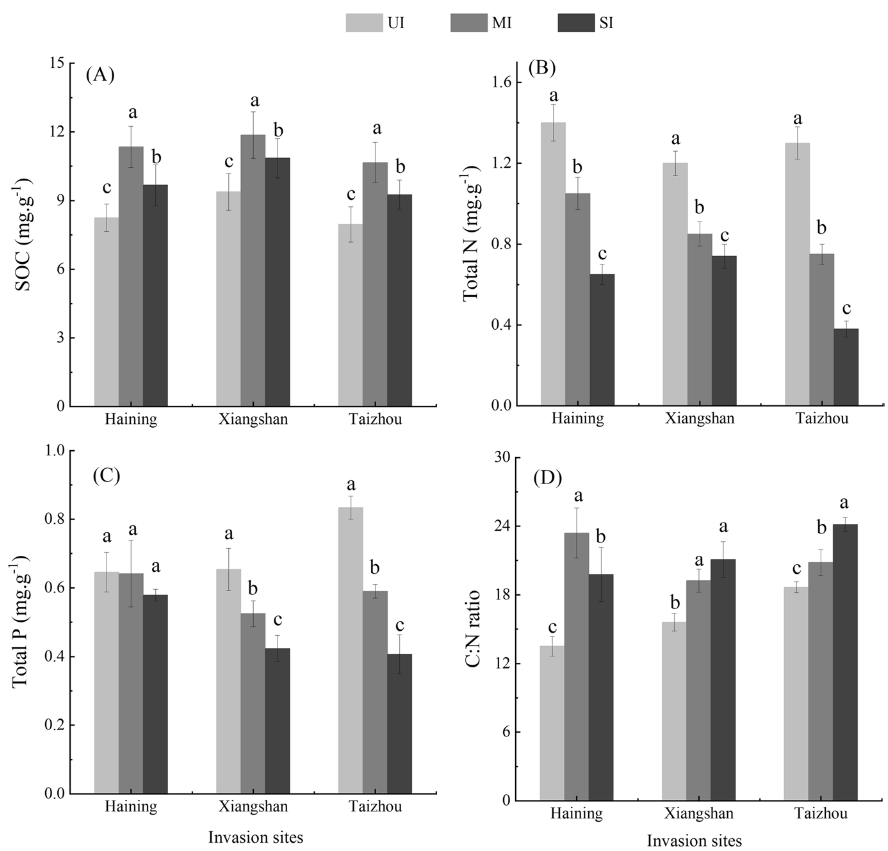


**Fig. 3** Association of goldenrod invasion severity with soil chemical nutrients in coastal shelterbelt forests. UI means uninvaded, MI means moderately invaded, SI means severely invaded. Different letters within the same sites indicate significant differences between SOC (soil organic carbon), Total N, Total P (total nitrogen), and C:N ratio (carbon: nitrogen ratio) among invasion severities ($P<0.05$), ($N_{UI}=36$, $N_{MI}=30$, $N_{SI}=27$)

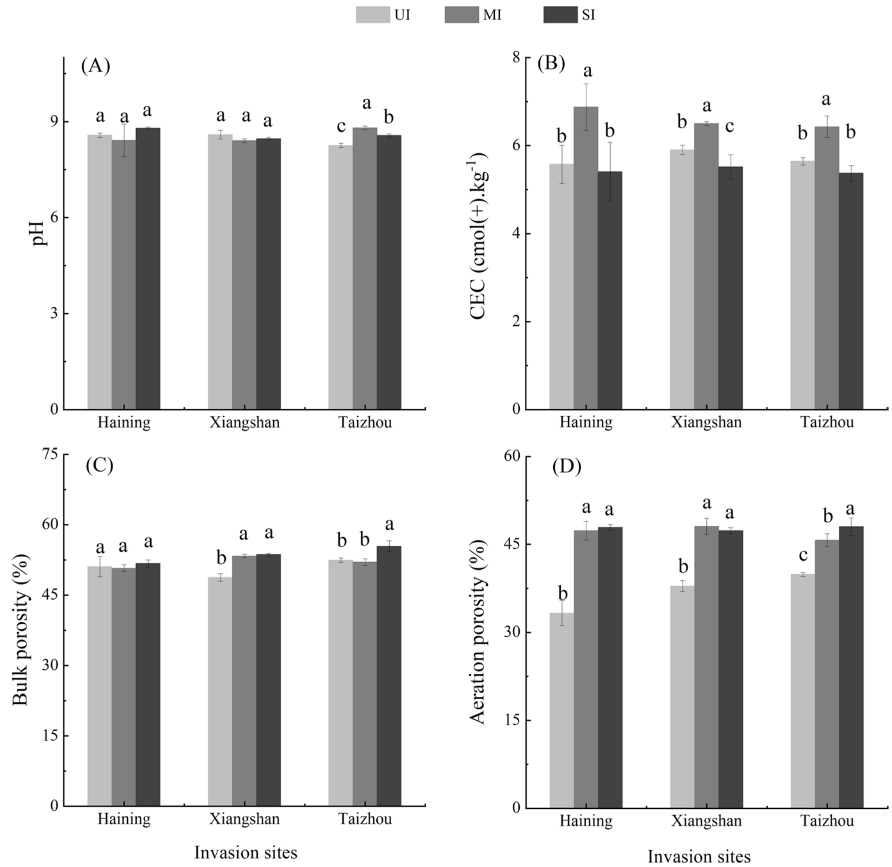


**Fig. 4** Association of goldenrod invasion severity with soil nutrient cycling and related physical properties in coastal shelterbelt forests. UI means uninvaded, MI means moderately invaded, SI means severely invaded. Different letters within the same sites indicate significant differences between soil pH, CEC, bulk porosity, and aeration porosity among invasion severities ($P < 0.05$), ($N_{UI} = 36$, $N_{MI} = 30$, $N_{SI} = 27$)

Effects of goldenrod invasion on the relationship between understory plant diversity and soil properties

RDA results (the total variation was 3.82 and the explanatory variables accounted for 60.0%) showed that soil total N and total P had strong positive effects on community stability and understory plant richness while negatively impacting species evenness (Fig. 5). Moderate goldenrod invasion slightly altered the relationship between soil nutrients and understory plant diversity, while severe goldenrod invasion remarkably reduced their correlational relationships. This was evidenced by the reduced number of significant correlations and the decreasing correlation coefficients in severely invaded plots compared to uninvaded plots (Fig. 6D). Goldenrod invasion specifically decoupled the correlations between species richness, Margalef index, Pielow index soil C:N ratio, and AP, separately. More importantly, it altered the correlational relationships between community stability and soil total P, total

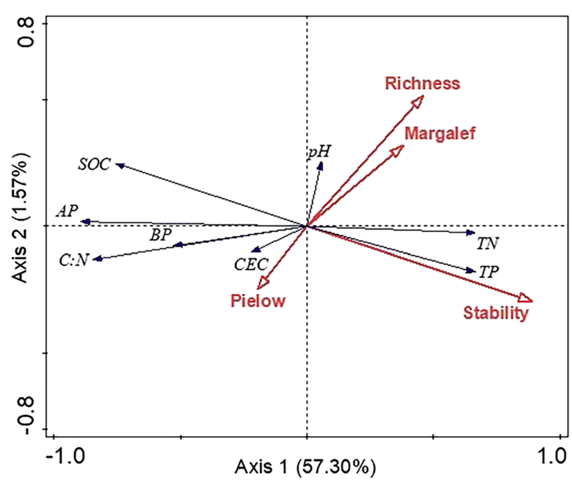


**Fig. 5** Effects of soil physiochemical properties on understory plant diversity based on Redundancy Analysis (RDA). SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; C: N ratio: carbon: nitrogen ratio; CEC: cation exchange capacity; BP: bulk porosity; AP: aeration porosity; Richness: species richness; Margalef: Margalef index; Pielow: Pielow evenness index; Stability: community stability index

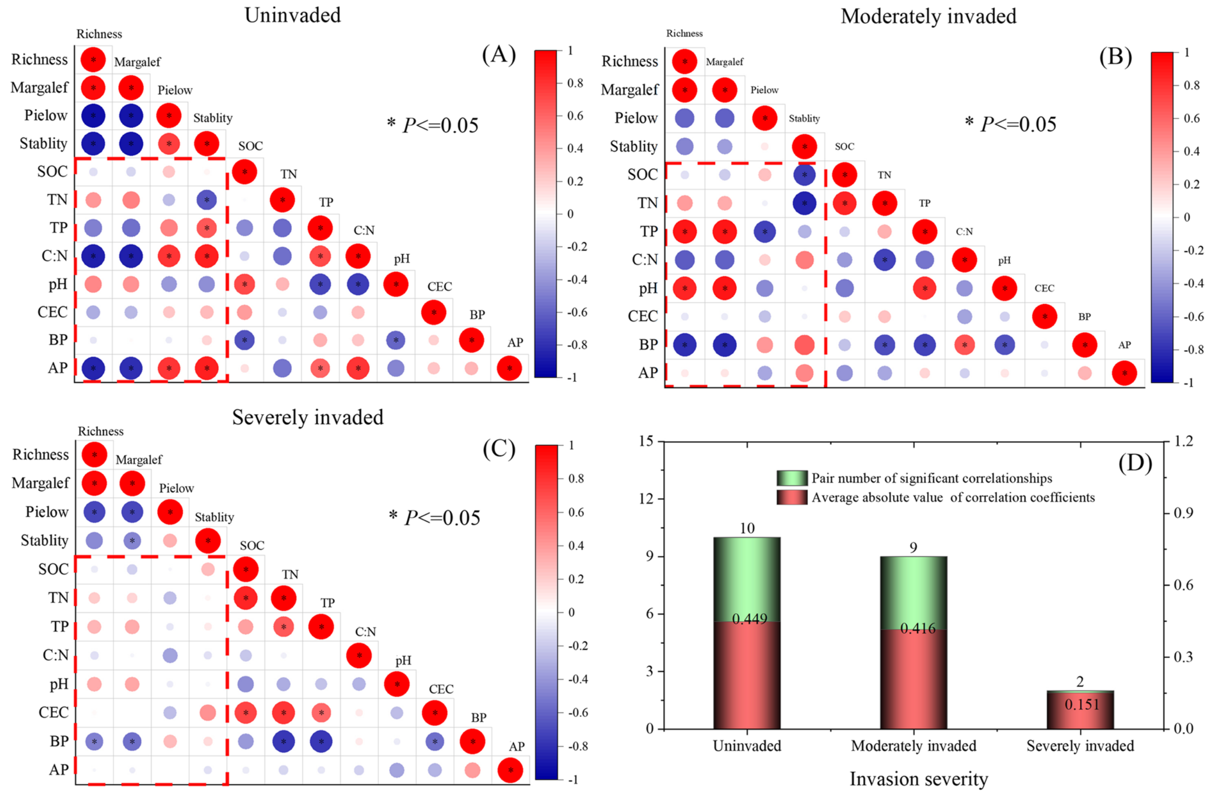


**Fig. 6** Effects of goldenrod invasion on the relationships between understory plant diversity and soil physiochemical properties. The dotted box emphasizes community-soil relations. Data are Pearson correlation coefficients with a significant level at $P < 0.05$. SOC: soil organic carbon; TN: total nitrogen; TP: total phosphorus; C: N ratio: carbon: nitrogen ratio; CEC: cation exchange capacity; BP: bulk porosity; AP: aeration porosity

N, C:N ratio, and AP, implying that goldenrod invasion altered the functioning of the plant community-soil nutrient system (Fig. 6A, B, C).

## Discussion

Invasion by nonnative plants is a complicated and multi-factored process, including traits of the introduced species (species invasiveness), the resident community (i.e., community invisibility), the disturbance history and regimes, and characteristics that comprise the introduction events (i.e., propagule pressure) (Liu et al. 2017). Factors such as light, soil nutrients, disturbance, local plant assemblages, land-use history, and eco-physiological characteristics of invasive plants can help determine successful invasion (Pyšek et al. 2009; Occhipinti-Ambrogi 2007). In this study, the severity of goldenrod invasion was associated with alterations to understory plant taxonomic diversity, community stability, and soil physiochemical properties. Overall, goldenrod invasion was associated with decreased species diversity and community stability but increased evenness in Chinese flame tree dominant mixed coastal shelterbelt communities. Further, reductions in soil nutrient availability was also associated with goldenrod invasion.

Goldenrod is capable of asexual reproduction and is highly adaptable to various ecological environments (Lu et al. 2007). It produces allelochemicals that result in goldenrod-dominant herbaceous communities (Abhilasha et al. 2008; Yuan et al. 2012), driving diversity loss at local scales (Uesugi and Kessler 2013; Hejda et al. 2009). Decreased plant diversity and increased evenness were observed with increasing levels of goldenrod invasion. Goldenrod invasion probably excluded the previous dominant herbaceous species and provided opportunities for other dominant species to expand, thus increasing species evenness in short timeframes, but the long-term response remains unclear. Our findings add evidence to previous studies where competition for growing space by goldenrod reduces species richness and increases evenness in plant communities (Groot et al. 2007; Meiners et al. 2001; Fenesi et al. 2015). Thus, this finding is consistent with our first hypothesis that goldenrod invasion severity would be negatively associated with species richness.

Plant invasion also alters soil properties, including chemical nutrients and hydraulic processes. Indeed, enhanced nutrient uptake has been suggested as a trait of highly invasive plants (Liao et al. 2011; Dassonville et al. 2008). In this study, moderate invasion of goldenrod increased SOC content, but severe invasion decreased SOC. This is somewhat consistent with other published works (Lenka et al. 2019; Hu et al. 2021). The reverse "U pattern" of SOC in our study is probably indicative that initial goldenrod invasion resulted in the death of some plant species, which was conducive to the increasing total SOC. But as goldenrod abundance increased to severe infestation levels, SOC decreased, this probably resulted from the residual effect of moderate invasion killing or excluding most vulnerable understory plant species, while increased invasion severity had little additional impact on the community. Thus, reductions in the input of organic matter into the soil in severely invaded plots likely reduced SOC. This hypothesis is supported by the mass-ratio hypothesis emphasizing the functional role of dominant species (Le Bagousse-Pinguet et al. 2019).

Increased goldenrod invasion was associated with reductions in both soil N and P. This may demonstrate substantial uptake of N and P by goldenrod, which may impact the establishment, growth, and fecundity of other understory plants, resulting in fundamental changes to nutrient cycling and the functionality of plant communities. Although the status of plant nutrients is outside the scope of this study, sites with plant invasions have been associated with higher aboveground biomass and standing stock of nutrients (Dassonville et al. 2008). Higher soil C:N ratios are commonly expected to reflect decreased N availability to plants, we found moderate goldenrod invasions improved C:N ratio at all three study sites and was especially evident in Haining. The C:N ratio of Haining (13.5) in invaded forests was lower than Xiangshan (15.6) and Taizhou (18.6), meaning that N mineralization and release in Haining were faster than the other two sites. When moderately invaded, Haining showed a dramatic increase in C:N ratios, but severe invasion decreased C:N ratios afterwards (Gerald 2019). In contrast, Xiangshan and Haining had similar patterns of increasing C:N ratios with greater severity of goldenrod invasion. This illustrates a slower N mineralization rate but likely an equilibrium state between mineralization and immobilization (C:N ratio between 20 to 30) (Graaff et al. 2006; Rudisill et al. 2015).

Soil aeration is important for maintaining soil nutrients, but excessive aeration accelerates soil nutrient loss (Singh et al. 2016). In this study, goldenrod invasion was associated with increased bulk porosity and aeration porosity. This alteration to soil physical properties may be attributed to the well-developed root system of goldenrod, which may alter soil porosity via root expansion (Wei et al. 2020). Additionally, higher soil porosity can enhance nitrification resulting in N loss from soil, which impairs the efficiency of nutrient uptake (Balaine et al. 2015). Our finding suggests that soil CEC and the severity of goldenrod invasion is a complicated and interacting process. In moderately invaded plots, soil CEC was higher than in uninvaded plots; however, severely invaded plots were associated with reduced CEC with levels at or below those of uninvaded plots. Soil CEC is also affected by soil structure, if goldenrod invasion modifies soil structure with its root system, the effects of roots and microbial activities, including allelochemicals may subsequently alter soil CEC (Zhang et al. 2009b; Chambers et al. 2014). Soil pH is another significant factor influencing CEC, but pH was non-responsive to goldenrod invasion except in Taizhou. These findings support our second hypothesis that goldenrod invasion alters soil nutrient availability. Our results also provide evidence that goldenrod can successfully invade the coastal communities of Eastern China, where the soils are highly alkaline ($pH > 8$). This finding is inconsistent with findings from Zhang et al. (2009a), suggesting that goldenrod invasions were predominately found on neutral or acidic soils, being sensitive to increased levels of NaCl. Therefore, goldenrod may be more adaptative to saline-alkali soil than previously determined.

Our study suggests that soil total N and total P are important factors for determining community stability and understory plant species richness in goldenrod invaded shelterbelt forests. But goldenrod invasion decoupled the correlational relationships between plant community diversity and soil physiochemical properties. The relatively balanced relationships of the original plant community-soil nutrient system were potentially disrupted by the invasion of goldenrod. For instance, in the uninvaded plots, understory plant richness was significantly related to soil C:N ratio and AP, and because higher AP values are conducive to water penetration, ventilation, and rootage, AP subsequently benefits understory species richness. But higher soil C:N reflects N deficiency, thus soil C:N was negatively correlated with understory plant richness but was positively related to evenness. This is likely because N deficiency decreased understory plant richness while the few surviving species formed new communities that were more even in composition (Graaff et al. 2006; Zhang et al. 2019). In goldenrod invaded plots, these correlations were decoupled, we assume this is the result of the novelness of the community, which require time to develop a relatively stable functional status. These findings are consistent with our third hypothesis (Zhang and Wan 2017; Gusev 2018). It is important to note that field observations also suggest that goldenrod invasion was highest near the seaside edge of the coastal shelterbelts, further indicating its potential adaptability to saline soils where many plant species are limited by high salinity. This study provides correlational evidence that goldenrod could drive changes in plant communities via alterations in soil physiochemical properties. Additional studies are needed to experimentally determine the causal relationships between goldenrod invasion, soil nutrients, and soil physical properties in coastal shelterbelt ecosystem.

## Conclusion

Goldenrod invasion caused declines in of understory plant diversity and reductions in soil nutrient availability in coastal shelterbelt forests of subtropical China. Moderate invasions were related to significant declines in plant diversity, which implies the need for forest managers to control goldenrod early in its invasion. Moderate goldenrod invasion was also negatively associated with soil nutrient availability as indicated by increased C:N ratio but decreased total N in all sites, indicating wide-ranging influences of goldenrod invasion on the coastal shelterbelt ecosystem. Not surprisingly, severe invasions further decreased plant taxonomic diversity and soil nutrient accumulation. By comparing the relationships between understory plant diversity and soil physiochemical properties with different degrees of invasion severity, we found that goldenrod invasion impacted these above- and below-ground plant-soil interactions, thus uncoupling ecosystem functioning. According to our study, goldenrod has increased its adaptability to highly alkaline soils, which may allow them to colonize more diversified ecosystems, increasing the challenge to control goldenrod invasions and expanding their potential impact. Our research also highlights the need to promote Early Detection and Rapid Response (EDRR) programs for goldenrod to prevent introductions and prioritize management in early stages.

**Acknowledgements** We are grateful to Shenhua Gu, Xuefeng Lin, and Quanxin Zhang for their assistance in the fieldwork. The research was supported by the National Key Research and Development Project (2019YFE0118900), the National Natural Science Foundation of China (32101506), the cooperative program in forest science between Zhejiang Province and the Chinese Academy of Forestry (16204002), and Jiyang College of Zhejiang A&F University under Grant No. RQ1911F09.

**Author contribution** H.X. carried out the fieldwork and laboratory analysis, prepared figures, and wrote the manuscript. L.P.K and G.G.W revised the manuscript; M.Y. contributed substantially to the study design and supervised the field and laboratory personnel.

**Data availability** Data are available on request from the authors.

**Declarations**

**Conflict of interest** The views and conclusions in this document are those of the authors and should not be interpreted as representing the opinions or policies of the funding agencies and supporting institutions. The authors declare that they have no conflict of interest.

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