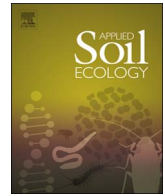




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# The invasive plant *Impatiens glandulifera* affects soil fungal diversity and the bacterial community in forests

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## ABSTRACT

Invasive plants may severely impact native biodiversity and ecosystem functioning. We examined potential effects of the invasive annual plant *Impatiens glandulifera* Royle on soil fungal and bacterial communities in temperate forests. Using a space-for-time approach, we established 72 plots in forest areas invaded by *I. glandulifera* and in forest areas, which were not yet invaded, equally distributed over three coniferous and three deciduous forests. In each plot, we determined plant species richness and abundance in the above-ground vegetation as well as the diversity and composition of the soil fungal community using T-RFLP analysis. Biolog Ecoplates were used to assess the activity of soil bacteria. The invasion of *I. glandulifera* caused significant shifts in plant species composition. Invaded plots were characterized by a higher diversity and an altered composition of the soil fungal community and by a lower soil bacterial activity in late spring. Carbon substrate utilization patterns of soil bacteria were also changed in invaded plots. Our experiment shows that *I. glandulifera* can modify soil fungal and bacterial communities, indicating an indirect effect of altered soil properties induced by the invasive plant, combined with the release of allelopathic compounds into the soil.

## 1. Introduction

The invasion of non-native species into natural habitats is considered as a major threat to native biodiversity (Pimentel et al., 2005; Pejchar and Mooney, 2009). Non-native species are key drivers of human-caused global environmental change and have the potential to affect ecosystems by altering native species diversity, community structure and interactions among organisms (Vilà et al., 2011; Pyšek et al., 2012; Stoll et al., 2012).

There is increasing evidence that “above-ground” biodiversity positively affects ecosystem functioning and services (Zavaleta et al., 2010; Isbell et al., 2011). In contrast, there is a gap in the knowledge of the role of “below-ground” diversity for ecosystem functioning. For example, Bardgett and van der Putten (2014) underlined the important role of the diversity of below-ground communities for shaping above-ground diversity and emphasized that the composition of the below-ground community might be more important than its species diversity for ecosystem functioning.

Soil fungi can be classified to be mutualistic, saprophytic, endophytic or pathogenic (Danielsen et al., 2012; Dighton, 2016). Soil fungi are a key component of below-ground communities and are

involved in a variety of microbiological and ecological processes influencing soil fertility, decomposition, cycling of minerals and organic matter (Ito and Reshi, 2013). Among them, mycorrhizal fungi, constituting a mutualistic symbiosis between soil fungi and plants, represent the main part of soil fungi in terms of biomass (Nehls, 2008) and play a crucial role for the establishment, survival and growth of vascular plants including trees and for the regeneration of forests (Courty et al., 2010; Simard et al., 2012).

Invasive plants are able to alter soil properties and soil processes (see reviews in Ehrenfeld, 2003; Raizada et al., 2008; Weidenhamer and Callaway, 2010). There is increasing evidence that invasive plants can affect species richness and composition of soil fungal communities (Callaway et al., 2004; Wolfe and Klironomos, 2005; Rodríguez-Echeverría and Traveset, 2015) and disrupt symbiotic associations between soil fungi and host plants (Ruckli et al., 2016). Hawkes et al. (2006) pointed out that alteration of the mycorrhizal fungal community may also be an effective mechanism through which plant invaders can affect ecosystem functions.

Beside soil fungal communities, alien plant species can also alter the activity and structure of soil bacterial communities (Kourtev et al., 2002; Lorenzo et al., 2013; Qin et al., 2014). Soil bacteria, together

Abbreviations: AMF, arbuscular mycorrhizal fungi; EMF, ectomycorrhizal fungi; LME, linear mixed-effect model; TRF, terminal restriction fragment; T-RFLP, terminal restriction fragment length polymorphism; OTU, operational taxonomic unit

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with soil fungi, play a key role in energy flow, nutrient cycling and organic matter turnover in ecosystems (Bauhus and Khanna, 1999). Because bacteria are very sensitive to changes in the environment, alterations in soil bacterial communities may precede and reflect changes in the whole ecosystem (Stefanowicz, 2006).

In our study, *Impatiens glandulifera* Royle (Himalayan balsam), an herbaceous annual plant belonging to the family Balsaminaceae, was chosen as focal invasive species. It is native in the western Himalaya and was introduced as garden ornamental plant to Europe and North America in the middle of the 19th century (Beerling and Perrins, 1993). It became naturalized and invasive in riparian and disturbed habitats (Hejda and Pyšek, 2006). In the last decades, *I. glandulifera* has increasingly invaded deciduous and coniferous forests, owing to natural and man-related disturbances (Nobis, 2008; Wagner et al., 2017). It is classified as one of the 100 worst alien species in Europe (DAISIE, 2009). *I. glandulifera* can cause slight changes in plant species richness and shifts in plant species composition in riparian habitats (Hejda and Pyšek, 2006; Diekmann et al., 2016), besides promoting soil erosion along riparian zones (Greenwood and Kuhn, 2014). In deciduous forests, *I. glandulifera* alters soil characteristics (Ruckli et al., 2013, 2014a; Rusterholz et al., 2014), gastropod communities (Ruckli et al., 2013) and soil invertebrate communities (Tanner et al., 2013; Rusterholz et al., 2014). Furthermore, this invasive plant reduces species richness and alters the composition of the soil seed bank with a delay of several years (Rusterholz et al., 2017). Leaves and roots of *I. glandulifera* contain an allelopathic compound (2-methoxy-1,4-naphthoquinone), which is released into the soil, having strong inhibitory effects on the growth of mycorrhizal fungi and on the germination of several native herbs (Ruckli et al., 2014b). Furthermore, forests invaded by *I. glandulifera* show a reduced mycorrhizal colonization of roots and thus a reduced survival of tree saplings (Tanner and Gange, 2013; Ruckli et al., 2014a, 2016; Pattison et al., 2016). These findings support the “novel weapons hypothesis”, which assumes that some invasive plant species produce secondary metabolites (allelochemicals) that are novel in their non-native ranges and that this novelty provides advantages to the invasive plant as it interacts with native plants, microbes or generalist herbivores (Callaway and Ridenour, 2004). The lower level of mycorrhizal colonization of native plant roots in invaded soils suggests that *I. glandulifera* can effectively change the mycorrhizal fungal community, but studies providing direct evidence for alteration in diversity or composition of soil fungal communities are so far lacking.

The majority of studies investigating the impact of invasive plants on soil fungal communities were carried out in grassland ecosystems (e.g. Hawkes et al., 2006; Mummey and Rillig, 2006; Zubek et al., 2016). However, some studies examined the effects of invasive plants on mycorrhizal fungi in forests situated in Asia (Niu et al., 2007) and North-America (e.g. Yamasaki et al., 1998; Stinson et al., 2006; Callaway et al., 2008; Wolfe et al., 2008; Barto et al., 2011). For example, Barto et al. (2011) showed that the invasive *Alliaria petiolata* does not change mycorrhizal fungal richness but alters their species composition in the community. However, knowledge about the impact of invasive plants on soil fungi in Central European forests is still limited.

The aim of this study was to examine the impact of *I. glandulifera* on the diversity of soil fungi and soil bacterial communities in deciduous forests dominated by *Fagus sylvatica* L. and in coniferous forests dominated by *Picea abies* (L.) H. Karst. or *Abies alba* Mill., the most abundant forest types in Switzerland and Central Europe. We established plots in forest areas with dense stands of *I. glandulifera* and plots in forest areas that were not yet colonized by the invasive plant to compare soil fungal and soil bacterial community. We applied terminal restriction fragment length polymorphism analysis (T-RFLP; see review in Thies, 2007; examples in Mummey and Rillig, 2006; Barto et al., 2011), a well established method to assess the genetic diversity and composition of soil fungal communities and used Biolog Ecoplates to estimate the activity of soil bacterial communities (Stefanowicz, 2006; Lorenzo et al., 2013;

Qin et al., 2014). In particular, we tested the following hypotheses: The invasion of *I. glandulifera* 1) reduces species richness of soil fungi and 2) causes shifts in the composition of the fungal community. *I. glandulifera* 3) increases the activity and 4) alters the composition of the soil bacterial community.

## 2. Material and methods

### 2.1. Study sites and design of the survey

The experiment was conducted in six study sites situated in a forest 15 km south of Basel, Northwestern Switzerland (47°26' N, 7°33' E). This region has a mean annual temperature of 9.4 °C and an annual precipitation of 947 mm (MeteoSwiss, 2016). The study sites were located within an area of 1.9 km × 1.0 km, with a distance of 100–840 m (mean 600 m) between each other. Elevation of the study sites ranged from 378 to 433 m a.s.l. Three study sites were located in stands dominated by *Picea abies* or *Abies alba* (hereafter referred to as ‘coniferous forests’), the other three in stands dominated by *Fagus sylvatica* (hereafter referred to as ‘deciduous forests’). The forest was affected by the windstorm Lothar in 1999. *I. glandulifera* started to invade several sites shortly after the storm in spring 2000. In spring 2015 (15 years after the beginning of the invasion), we selected a 15 m × 25 m area invaded by *I. glandulifera* (hereafter referred to as “invaded area”) in each study site. An area of the same size which was not yet colonized by the alien plant (hereafter referred to as “uninvaded area”) was chosen in proximity to the corresponding invaded one (mean distance between invaded and uninvaded area 50 m, range 30–80 m). Pairs of invaded and uninvaded areas did not differ in elevation, inclination, exposition, forest type and forest management (Table S1 – Electronic Supplementary material). In each invaded area, we installed six randomly chosen 1 m × 1 m plots which had a similar cover of *I. glandulifera* (Table S2). Similarly, six 1 m × 1 m plots with an equal spatial distribution were installed in the corresponding uninvaded areas. This resulted in a total of 72 plots (six plots × two invasion states [invaded and uninvaded areas] × six sites [three in coniferous and three in deciduous forests]). Thus, our experimental design followed a space-for-time substitution approach (Pickett, 1989; Diekmann et al., 2016). The uninvaded areas are assumed to represent the situation prior to the invasion of *I. glandulifera*. In 2017, two years after the present study, two of the formerly uninvaded areas were partially colonized by *I. glandulifera*, showing that both our invaded and uninvaded areas provide suitable habitat for the invasive species.

### 2.2. Data collection

To assess the seasonal impact of *I. glandulifera* on diversity and composition of the soil fungal community, we collected soil samples in each plot four times in the course of the vegetation period: 2/3 June (juvenile plants), 27/28 July (flowering plants), 29/30 September (fruiting plants) and 1/2 December 2015 (partly decomposed plants). At each sampling occasion, three randomly chosen soil samples were collected in each 1 m × 1 m plot using a soil corer (depth 5 cm, diameter 5.05 cm, volume 100 cm<sup>3</sup>). The three samples of a plot were pooled and mixed, resulting in a total of 288 samples (72 plots × four sampling occasions). Soil samples were transported on ice to the laboratory, where they were sieved (mesh size 2 mm) and stored at –80 °C for further analyses. At each sampling occasion, the density, height and biomass of *I. glandulifera* were assessed in additional plots of 20 cm × 20 cm adjacent to the invaded plots.

The cover of each plant species belonging to the above-ground vegetation (herbs and woody plants up to a height of 50 cm) was visually estimated using the Domin scale (Mueller-Dombois and Ellenberg, 2002) in each 1 m × 1 m plot at the end of May 2016. In addition, total cover of ground vegetation, mosses, leaf litter, dead wood and bare ground were visually estimated (accuracy 5%) and the mean and

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