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Invasion by *Solidago* species has limited impacts on soil seed bank communities

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Abstract

Increasing attention in invasion biology is being paid to measuring and understanding the impacts of invasive species. For plant invasions, however, the impact of invasion on soil seed bank communities has been under-studied. At six sites in southern Germany, we investigated whether areas invaded by *Solidago gigantea* and *Solidago canadensis* experienced a reduction in seed bank species richness, size and diversity, and a change in species composition compared to adjacent uninvaded areas. We found no overall effect of invasion on seed bank size, or on species richness and diversity. Seed bank size significantly decreased from 0–5 cm to 5–10 cm depth in both invaded and uninvaded areas. A significant amount of variation in species composition was explained by invasion, but it was only one-tenth of that explained solely by site effects. Our study suggests that invasion by *Solidago* species may not have the same impacts on the soil seed banks of native species as other invasive perennial forbs that have so far been studied.

Zusammenfassung

In der Invasionbiologie wird dieserzeit vermehrtes Augenmerk darauf gerichtet, die Auswirkungen invasiver Pflanzenarten besser einzuschätzen und verstehen zu können. Welche Auswirkungen invasive Pflanzenarten auf die Samenbanken von Pflanzengemeinschaften haben, wurde in diesem Kontext bisher allerdings nur unzureichend untersucht. Im Süden Deutschlands wurde an sechs Standorten unterschiedlicher Habitattypen untersucht, ob Samenbanken durch die Invasion von *Solidago gigantea* und *S. canadensis* eine Reduktion des Artenreichtums, der Größe oder der Diversität erfuhren und auch, ob sich die Artenzusammensetzung innerhalb der Samenbanken durch die Invasion veränderte. Die Samenbanken der invadierten Standorte wurden hierfür mit angrenzenden, nicht-invasierten Standorten verglichen. Insgesamt zeigte die Invasion keinen Effekt auf die Größe der Samenbanken, den Artenreichtum oder die Artenvielfalt. Sowohl in invasierten als auch nicht-invasierten Standorten nahm die Größe der Samenbanken mit zunehmender Tiefe von 0-5 cm zu 5-10 cm signifikant ab. Ein signifikanter Anteil der Variation in der Artenzusammensetzung konnte durch die Invasion erklärt werden, ein Zehntel hiervon allerdings wurde durch Standorteffekte bedingt. Unsere Studie deutet darauf hin, dass die Invasion von *Solidago* Arten nicht die gleichen Auswirkungen auf die Samenbanken einheimischer Arten haben wie die anderen invasiven mehrjährigen Stauden, die bisher untersucht worden sind.

Keywords: Legacy effect; Exotic; Goldenrod; Invasive species

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Introduction

Recently, increasing focus in invasive-plant ecology has been given to identifying and measuring the impacts of invasive plants on native plant species and ecological processes (Davis et al., 2011; Vila et al., 2011). A large number of invasive-plant impact studies have focused on the effects of invasion on native plant species abundance, richness and diversity, with overall negative effects shown across multiple taxa (Vila et al., 2011), presumably as a consequence of competition and suppression by the alien species. While multiple studies have considered impacts of invasive plants on native plant diversity and composition aboveground, relatively few studies have focused on the indirect impact of invasive plants on native species through changes in soil seed banks (Gioria, Pyšek, & Moravcova, 2012), despite their ecological importance (Thompson, Bakker, & Bekker, 1997). Restoration efforts after invasive species removal may require additional seed input if seed banks are depleted or strongly different in species composition.

Invasive species may impact soil seed banks via several potential mechanisms. Many invasive plants form tall, dense stands that may restrict the suite of species able to survive, grow and produce seeds under high shade. They may also act as strong physical barriers to seed dispersal into seed banks. Allelopathy (del Fabbro, Güsewell, & Prati, 2014), changes in organic matter deposition, soil moisture and nutrient content and rates of decomposition (Dassonville et al., 2008; Scharfy, Eggenschwiler, Venterink, Edwards, & Güsewell, 2009) can occur in soils of invaded habitats, which may lead to an increased rate of viable seed loss from seed banks.

Solidago canadensis and *Solidago gigantea* are two invasive and now widespread alien species occurring throughout Europe, often in near-monospecific stands in a variety of habitats. Despite being well-known invaders, we are aware of no study that has assessed the effects of *Solidago* on seed bank diversity and composition in invaded areas. We assessed abundance, species richness, diversity and composition in soil seed banks under areas invaded by *S. gigantea* and *S. canadensis*, and compared them to soil seed banks in adjacent uninvaded areas of vegetation. Our main hypotheses were:

(1) The abundance, richness and diversity of species in the soil seed bank will be reduced in invaded areas compared to uninvaded areas.
(2) The composition of species in the soil seed bank will differ in areas invaded by *Solidago* spp., compared to areas uninvaded.
(3) Soils from invaded areas will have a greater *Solidago* abundance than uninvaded areas. If persistent viable seed banks are not formed, then *Solidago* abundance should decline strongly with increasing soil depth (with increasing depth acting as a surrogate for increasing soil age). We had *no a priori* expectations regarding how the effects of invasion on native species seed banks might be affected by soil depth.

Material and methods

Study sites and soil collection

Six sites were chosen for soil collection from areas of vegetation that were either invaded or uninvaded by *Solidago* species in the vicinity of the city of Constance in Baden-Württemberg, Southern Germany (Table 1). The oldest herbarium record for *S. gigantea* in Germany dates to the first half of the 19th century, while *S. canadensis* was first recorded in 1857, and both species are now widespread in the Central Europe (Weber 1998; Weber & Jakobs 2005). Both *S. gigantea* and *S. canadensis* are known to be tolerant of a broad range of habitat types, and *S. gigantea* in particular is known to invade habitats with wetter soils (Sebald, Seybold, Philippi, & Woerz, 1996; Werner, Bradbury, & Gross, 1980). Thus, the six sites were chosen to reflect a range of habitat types where *S. gigantea* (all six sites) and *S. canadensis* (two of the sites) have invaded, including wet meadows with tall native herbs, *Carex* spp. and *Phragmites australis*, and anthropogenic habitats (Table 1).

In April 2013, soil samples were obtained from the six sites. At each site, an area of vegetation invaded by *Solidago*, and an adjacent uninvaded area were identified. The invaded areas were clearly distinguishable, due to the presence of dead *Solidago* aboveground biomass from the previous year and emerging new shoots. Spatial proximity of invaded and uninvaded areas should minimise differences in environmental conditions due to factors other than invasion. At each site, the invaded patches were all larger than 50 m^2, and five out of six sites had invaded patches >100 m^2. The maximum distance between an invaded and uninvaded quadrat was ~50 m. Seed banks were sampled in each invaded and uninvaded area per site, within three, evenly spaced (5–10 m distance) replicate quadrats (2 m × 2 m). The quadrats were systematically placed in order to obtain a representative set of soil seed bank samples across each invaded and uninvaded area. Within each quadrat, five replicate soil cores of 10 cm depth were taken, using a 5 cm diameter soil-corer. The five samples were taken from close to each corner and from the centre of each quadrat in order to capture small-scale spatial variability that is common in soil seed banks. The soil cores were split *in situ* into two depths: 0–5 cm and 5–10 cm depth, so that we could assess variation in *Solidago* and non-*Solidago* species abundance, and species composition according to soil depth. The five core samples of each depth within a quadrat were bulked. Thus, with six sites, we obtained a total of 36 soil seed bank samples overall and per soil depth (six sites × two (invaded and uninvaded areas per site) × three quadrats per invaded/uninvaded area within a site). The soil samples were stored at 6 °C until all samples were collected (≤3 days).