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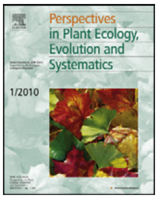

Research article

# Eco-evolutionary litter feedback as a driver of exotic plant invasion

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ABSTRACT

Many studies have examined positive feedbacks between invasive plant traits and nutrient cycling, but few have investigated whether feedbacks arise from introduction of pre-adapted species or from eco-evolutionary feedback that develops after introduction. Eco-evolutionary feedback could occur between an invader's leaf tissue C:N ratio and its response to litter accumulation. Previous modeling predicts that occurrence of this feedback would be reflected by: (1) field data showing higher litter:biomass ratios in the invasive range; (2) high C:N genotypes benefiting more from experimental litter additions than low C:N genotypes; (3) this beneficial effect on high C:N genotypes inducing a critical transition toward invader dominance when a critical amount of litter is added to a native species-dominated community experiencing low nutrient conditions. Here, we empirically tested these predictions for the invasive grass *Phalaris arundinacea*, which has undergone post-introduction evolutionary change toward attaining higher C:N ratios under high nutrient conditions. We performed a biogeographical comparison of litter:biomass ratios in the native (Europe) and invasive (USA) range, and an experiment with mesocosms from the invasive range under low nutrient conditions. Low and high C:N *Phalaris* genotypes were introduced into native-dominated and bare mesocosms, to which varying litter amounts were added. The biogeographical comparison revealed that litter:biomass ratios were higher in the invasive range. The mesocosm experiment showed that when grown in isolation, only high C:N genotypes responded positively to litter. This effect, however, was not strong enough to stimulate *Phalaris* when exposed to competition with native species. Our results suggest that eco-evolutionary feedback between *Phalaris*' C:N ratio and litter accumulation could occur, but only under high nutrient conditions. Our experiments suggest that eco-evolutionary feedback may select for specialist rather than superior genotypes. Hence, genotypic variation induced by post-introduction admixture may be subject to context-dependent selection due to eco-evolutionary feedback, increasing trait variation within invasive populations.

## Introduction

Successfully established exotic plants may actively modify the habitats in their new range, which induces cascading effects on ecosystem functioning (Jones et al., 1994; Crooks, 2002; Cuddington and Hastings, 2004; Cuddington et al., 2007). In this context, much attention has been paid to invasive plants affecting nutrient cycling, thereby changing the partitioning of carbon and nutrients between soil, litter and living biomass pools (Vitousek et al., 1987; Witkowski, 1991; Ehrenfeld, 2003). Many examples highlight the potential for invasive species to accelerate nutrient cycling, but invasive species may decelerate nutrient cycling as well (Liao et al., 2008; Ehrenfeld, 2010). Both acceleration and deceleration of nutrient cycles may induce a positive feedback in the invasion process if the net effect of the ecosystem change is beneficial to the invader itself (Hobbie, 1992; Allison and Vitousek, 2004; Eppinga et al., 2011).

Another line of research suggests that post-introduction evolution of exotic plants may contribute to their success (Müller-Schärer et al., 2004; Bossdorf et al., 2005; Strayer et al., 2006). Post-introduction evolution may be driven by altered selection pressures in the new range. Possible factors altering selection pressure include different environmental conditions (Sakai et al., 2001; Leger and Rice, 2007), release from natural enemies (Blossey and Nötzold, 1995; Blair and Wolfe, 2004), and lack of co-evolution with newly encountered competitors (Bais et al., 2003; Callaway and Ridenour, 2004). Post-introduction evolution may be more likely when there have been multiple introduction events of a species into the new range, resulting in admixture between subpopulations that are isolated from each other in the native range

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(Lavergne and Molofsky, 2007; Culley and Hardiman, 2009). As a result, novel genotypes may arise that differ with regard to their ability to modify habitats, affecting the strength and nature of influence exotic plants exert on ecosystem functioning in their invasive range versus their native range. This creates the possibility of an eco-evolutionary feedback, which comprises the invader altering its environment and subsequently evolving in response to these changes (Lewontin, 2000; Post and Palkovacs, 2009; Bailey, 2011). Eco-evolutionary feedback provides a possible explanation for why some invasive species perform better in their invasive range (Hierro et al., 2005). Importantly, the mechanisms described above may induce these evolutionary changes over very short timescales (Whitney and Gabler, 2008).

Until now, the role of post-introduction evolution has received little attention in empirical studies of invasive plants and nutrient cycling. Positive eco-evolutionary feedback would occur when a newly evolved genotype (from here referred to as 'invasive genotype') affects nutrient cycling in a way that creates more favorable conditions for this novel genotype than genotypes originating from the native range (from here referred to as 'native genotypes') or other plant species. Previous studies of eco-evolutionary feedback between organisms and resource dynamics have been mainly theoretical modeling exercises (Laland et al., 1999; Odling-Smee et al., 2003; Kylafis and Loreau, 2008). A notable exception, however, is a number of studies showing that there is a genetic basis for variation in tannin concentrations in the leaves of *Populus* spp. (Schweitzer et al., 2004), which may affect nutrient cycling in its native habitat (Schweitzer et al., 2005; Pregitzer et al., 2010; Smith et al., 2012). In this system, there may be positive eco-evolutionary feedback because the genotypes decelerating nutrient cycling show a tendency toward increased production of fine roots (Fischer et al., 2006). Theoretical modeling suggests that similar eco-evolutionary feedback could occur between invasive exotic plants and nutrient cycling (Eppinga et al., 2011), but empirical evidence for the latter is even more scarce.

A key trait affecting nutrient cycling is the C:N ratio of the dead plant material becoming part of the litter or detritus pool (Hobbie, 1992; Hooper and Vitousek, 1998; Ehrenfeld, 2003). Although leaf tissue C:N ratio is strongly determined by nutrient availability (e.g. Hobbie, 1992), genotypic variation in uptake and allocation strategies can create differences in C:N ratio between genotypes at a given soil nutrient level. A previous model study suggests that post-introduction evolution toward higher C:N ratios could create a positive eco-evolutionary feedback in the invasion process (Eppinga et al., 2011). More specifically, genotypes with a higher leaf tissue C:N ratio could affect nutrient cycling by stimulating the accumulation of recalcitrant litter (e.g. Thormann et al., 1999), which may induce a positive eco-evolutionary feedback if genotypes with high C:N ratios also have higher growth rates under that litter. Although the main driver of trait variation seems to have been genetic recombination of previously isolated subpopulations (i.e., admixture; Lavergne and Molofsky, 2007), model analysis revealed that eco-evolutionary feedback could be a secondary feature exacerbating the invasion process (Eppinga et al., 2011). This model exercise yielded one prediction of how eco-evolutionary feedback would be reflected in field data, and two predictions of how eco-evolutionary feedback could be tested for experimentally (Eppinga et al., 2011). More specifically, occurrence of this eco-evolutionary feedback would be reflected by (see Appendix A for details): (1) field data showing higher litter:biomass ratios in the invasive range; (2) high C:N genotypes benefiting more from experimental litter additions than low C:N genotypes; (3) this beneficial effect on high C:N genotypes inducing a critical transition toward an invader-dominated state when a critical amount of litter is added to a native species-dominated community that is growing under low nutrient conditions.

The aim of this study was to empirically test these three model predictions, thereby examining to what extent exotic plant invasion could be driven by eco-evolutionary feedback between leaf tissue C:N ratio and litter accumulation. For this test we used the wetland grass *Phalaris arundinacea* (*Phalaris* from here), which is invasive in North America. Previous studies revealed that *Phalaris* is a weak competitor for nutrients but a strong competitor for light. Because decomposition of litter releases nutrients but reduces light availability, the presence of litter may increase the competitiveness of *Phalaris* (Perry and Galatowitsch, 2004; Perry et al., 2004; Eppinga et al., 2011). Also, novel genotypes occurring in the invasive range have higher C:N ratios than native genotypes when grown under the same (high) nutrient and light conditions (Lavergne and Molofsky, 2007; Eppinga et al., 2011).

First, we compared field observations of litter:biomass ratios in *Phalaris*-dominated plots in native and invasive ranges. Based on previous model predictions, we hypothesized that litter:biomass ratios are higher in the invasive range (Fig. 1A and B). Second, we measured the response to litter of low C:N and high C:N genotypes when grown in isolation. A requirement for eco-evolutionary feedback would be that the high C:N genotypes respond more positively to litter (Fig. 1C and D). Third, we introduced low and high C:N *Phalaris* genotypes into native species-dominated mesocosms with low nutrient conditions, which were then exposed to varying litter levels (Fig. 1E and F). For these conditions, previous model predictions suggest that occurrence of an eco-evolutionary feedback would be reflected by similar growth of low and high C:N genotypes under low levels of litter, but better growth of high C:N genotypes under high levels of litter (Eppinga et al., 2011; Fig. 1E and F).

## Material and methods

### Study species

*Phalaris arundinacea* (reed canary grass, *Poaceae*, *Phalaris* from here) is a cool season ($C_3$) grass that is one of the most aggressive invaders of North American wetlands (Galatowitsch et al., 1999; Lavergne and Molofsky, 2004; Zedler and Kercher, 2004). Evidence is accumulating that the success of this species is at least partly due to post-introduction evolution, which has been stimulated through multiple introductions of disparate European populations (Lavergne and Molofsky, 2007). Multiple introductions have lead to novel genotypes of smaller genome size, forming invasive populations with high genetic variability and phenotypic plasticity (Lavergne and Molofsky, 2007; Lavergne et al., 2010). Previous experiments show that invasive genotypes have on average a higher growth rate and a higher leaf tissue C:N ratio than native genotypes when grown under the same nutrient and light conditions (as further explained in the description of the experimental design of the mesocosm experiment).

### Field survey

#### Study areas

We studied four sites in *Phalaris*' native range (South Bohemia, Czech Republic), and four areas in its invasive range (Vermont, USA). The four sites in the native range were all in the vicinity of the town of Třeboň (1: Halámky 48°51′N, 14°54′E, 2: Krabonoš 48°48′N, 14°55′E, 3: Nová Hlína 49°02′N, 14°48′E, 4: Mokré Louky 49°01′N, 14°46′E). The climate in this region is sub-oceanic,