



## Context-dependent outcomes of subarctic grass-endophyte symbiosis



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### ABSTRACT

Symbiotic interactions are often context-dependent. We explored how different habitats have modified the symbiosis between the grass *Festuca rubra* and the endophyte *Epichloë festucae*. We grew endophytic and endophyte-free grasses originating from subarctic meadows and open river banks in a growth chamber with a hemiparasitic plant (*Rhinanthus minor*) and a competitor (*Achillea millefolium*), representing typical plant-plant interactions in meadows. Grasses from meadows were more adapted to plant species interactions than river bank grasses, and the presence of the endophyte strengthened this difference further. Endophyte-infected meadow grasses did not suffer from the hemiparasite, but the endophyte decreased the tolerance of the river bank grasses to the hemiparasite. Endophytic river bank grasses invested more than meadow grasses in vegetative spread. These results suggest differentiation of grass-endophyte symbiota between the habitats, and underline the context dependency of species interactions as well as the role of symbionts in the habitat adaptation of plants.

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### 1. Introduction

According to current views, species interactions are often highly context-dependent and may result in varied outcomes in different growth conditions along an antagonism-mutualism continuum (Chamberlain et al., 2014). The range of physical growth conditions together with different interacting species form a mosaic of variable selection pressures that may direct coevolution among plants and their symbionts towards mutualism in one place and antagonism in another (Saikkonen et al., 2004; Thompson, 2005; Chamberlain et al., 2014). The allocation of limited resources to different plant lifecycle functions, e.g. vegetative growth, reproduction, defence and mutualistic symbionts (e.g. Bazzaz, 1997) is likely to differ among habitats according to the dominant selective pressures. Plant individuals that are tolerant or resistant to negative plant-plant interactions are favoured in dense vegetation, while the lack of competition in severely ruderal habitats selects for tolerance against physiological stressors (Grime, 1977; Brooker and Callaghan, 1998).

In addition to the dominant species in a community, some seemingly unapparent organisms may act as the keystone species

shaping the structure and functioning of a plant community (Mallik, 2003). *Epichloë* endophytes and hemiparasitic plants are suggested to act like keystone species in grassland communities (Joshi et al., 2000; Omacini et al., 2001; Müller and Krauss, 2005; Bardgett et al., 2006; Houston and Wolff, 2012). Hemiparasitic plants are capable of photosynthesis but utilise resources from other plant species, using them as their hosts. Hemiparasites form plant-plant interactions that potentially affect community interactions in many additional indirect ways (Joshi et al., 2000; Bardgett et al., 2006). Hemiparasites reduce the growth of the host plant species and may thus alter the dominance relationships in vegetation (Press, 1998; Press and Phoenix, 2005; Hellström et al., 2011; Bao et al., 2015b). They may also increase species diversity in grassland communities where the dominant plant species are favourable hosts for the hemiparasite. In addition, microbial symbionts of plants have sometimes unexpected cascading effects on food webs (Müller and Krauss, 2005). Endophytic micro-organisms may increase the herbivore resistance of plants (reviewed in Rodriguez et al., 2009), and grass endophytes (the fungi, *Epichloë/Neotyphodium*) are particularly regarded as defensive mutualists for their host grasses (e.g. Clay, 1990; Schardl, 2001; Schardl et al., 2004). However, the studies on the role of these endophytic fungi in modifying plant species interactions has concentrated mainly on interspecific competition (e.g. Marks et al.,

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1991; Faeth et al., 2004; Rudgers and Orr, 2009; Cheplick et al., 2014; Bao et al., 2015a; but see Lehtonen et al., 2005).

In this work we studied the context dependency of plant-endophyte symbiosis. We tested how the *Epichloë* endophyte affects the plant-plant interactions of its wild grass host and whether the original habitat has shaped the reaction of endophyte-grass symbiota to these plant-plant interactions. We used native subarctic red fescue (*Festuca rubra* s.l.) and its shoot endophyte *Epichloë festucae* originating from two different subarctic habitats, semi-natural meadows and sandy river banks, as the study system. These habitats occur close to each other, forming a mosaic along subarctic rivers. The habitats differ dramatically in terms of their physical stress and vegetation density and thus have different selection pressures acting on plants, allowing us to evaluate the adaptation of the grass-endophyte symbiota to interspecific plant-plant interactions. We performed a growth chamber experiment with endophyte-infected (E+) and endophyte-free (E-) red fescues that originated from two habitat types (river bank or meadow) and grew the grasses with or without a parasitic plant, *Rhinanthus minor*, and with or without a competitor, *Achillea millefolium*, to study ecological multispecies interactions among these species. Our aim was to find out (1) if the interacting organisms (endophyte, parasitic plant and competitor) affect the performance and growth strategies of *F. rubra* grasses originating from two different habitats, and (2) if the endophyte status or original habitat of the host grass affects the performance of the parasitic plant and/or competitor. In addition, we gained information about (3) how the original habitat of the grass, the parasite and the competitor affect the intensity of endophyte infection within grass individuals.

## 2. Methods

### 2.1. Study species

*F. rubra* s.l. (Poaceae) (red fescue) is a perennial, widely distributed cosmopolitan grass that is common in many natural and human-influenced habitats. In Finnish Lapland, *F. rubra* grows mainly in meadows and on river banks and roadsides. *F. rubra* has a strong tendency to spread vegetatively with runners. *E. festucae* (Ascomycota; Clavicipitaceae) is a systemic endophytic fungus of fine fescues (*Festuca*) described by Leuchtmann et al. (1994) and has a high infection frequency in many *F. rubra* populations in Fennoscandia (Saikkonen et al., 2000; Bazely et al., 2007; Wäli et al., 2007). *E. festucae* may produce anti-insect alkaloids as well as anti-vertebrate alkaloids (Siegel et al., 1990; Leuchtmann et al., 2000). Transmission of *E. festucae* occurs vertically via host seeds (Leuchtmann et al., 1994). *E. festucae*-grass symbiosis has been used as an advantageous research model system (Schardl, 2001).

*R. minor* (Orobanchaceae) (yellow rattle) is an annual hemiparasitic plant with a broad host range (Gibson and Watkinson, 1989). It is common in open grasslands, e.g. roadsides, meadows and shorefront habitats in Europe, North America and Western Asia (Westbury, 2004). *R. minor* parasitises *F. rubra*, which is better as a host plant compared to several other grass species (Gibson, 1986; referred to in Westbury, 2004). *A. millefolium* (Asteraceae) (yarrow) is a perennial aromatic herb that has rhizomatous growth form. *A. millefolium* is a common species in the meadow habitats of northern Lapland. According to Gibson and Watkinson (1989), *R. minor* also forms haustoria with *A. millefolium*. However, herbs are generally considered poor hosts for parasitic plants compared to grasses and legumes due to their efficient resistance responses (Cameron et al., 2006, 2008; Rümer et al., 2007).

### 2.2. Habitats

The *F. rubra* plants were obtained from individuals originating from the Teno river valley in the northernmost part of Finland (69°N, 27°E) (Wäli et al., 2007). They were originally collected as seeds from nine populations representing two different habitats types: meadows (6 populations) and sandy river banks (3 populations). Populations were located along the riverside and the range between the most distant populations was c. 115 km (measured along the rivers). The two habitats differ in terms of competition, parasitism and physical growing conditions. In the meadows, more than 90% of the ground was covered by vegetation, whereas on the river banks less than 10% was vegetated (Wäli et al., unpublished data). All of the study species are very common in meadow habitats, whereas *F. rubra* is one of the few species that occurs on river banks. Biotic interactions (i.e. competition, parasitism, and herbivory) are likely to be strong selective factors affecting grass-endophyte symbiosis in meadows. On the river banks, the harsh physical conditions, i.e. low nutrient levels, moving ice, sand burial and flooding, represent more prominent selection pressures. The contents of organic matter and all soluble nutrients in the soil are significantly lower on the river bank than in the meadow (Wäli et al. unpublished data). Although the natural infection frequency of *E. festucae* in *F. rubra* populations is ca. 60% in the meadow habitats and ca. 20% on the river banks in the Teno river valley area, no genetic differentiation of the endophyte has been detected between these habitats (Wäli et al., 2007).

### 2.3. Experimental design

The endophyte status (infected/not infected) of the seed families collected from the natural populations was determined by staining and microscopic examination of at least five seeds from each family (Saha et al., 1988). To observe the direct effects of the endophyte separately from the effect of the *F. rubra* genotype (Saikkonen et al., 1998, 2004), the endophyte infection of the grass was manipulated (Saikkonen et al., 2010). Some of the naturally endophyte-infected (NE+) seeds were heat-treated to kill the endophyte and produce manipulatively endophyte-free (ME-) *F. rubra* individuals. This was done by heating the moist seeds in Eppendorf tubes in a water incubator at +54.2 °C for 20 min. Some of the naturally endophyte-free seedlings (NE-) were inoculated with endophyte hyphae using a method described by Latch and Christensen (1985) in order to obtain manipulatively endophyte-infected (ME+) *F. rubra* individuals. The endophyte strain used in the inoculations was isolated from the same grass population from which the grass seed was collected. First we tested if grasses with manipulated endophyte statuses differed from grasses with comparable natural endophyte statuses and we analysed the data for the grass performance with the endophyte manipulation taken into account (we compared ME+ with NE+ and ME- with NE-). Because manipulated endophyte statuses did not differ from the corresponding natural endophyte statuses, we combined the ME+ and NE+ plant groups as well as the ME- and NE- plant groups and used only the two endophyte infection levels in the final analyses (hereafter E+ and E-). This manipulation of the endophyte infection ensured that both endophytic and endophyte-free grasses were genetically similar and the effects of the endophyte were not connected to the grass lineage. We were not interested in the effects of the grass genotype or the original populations of the grasses on plant performance, so these factors were not included in the statistical models.

The experimental *F. rubra* individuals were maintained in a common garden in the Botanical Garden of the University of Turku (southwest Finland) for 6 yr. To obtain similar grass material for

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