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# The hemiparasite *Pedicularis palustris*: ‘Ecosystem engineer’ for fen-meadow restoration

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ABSTRACT

‘Ecosystem engineers’ have a critical role in the structure and function of natural communities and need to be considered as focal species to enable successful conservation or restoration of ecosystems. Through introduction and/or managing a single species, an entire community can be influenced. In our study we show that *Pedicularis palustris*, an endangered hemiparasite in large parts of Europe, can act as an ‘ecosystem engineer,’ speeding up the restoration of undrained fen-meadow ecosystems colonised by species-poor and resistant *Carex acuta* vegetation. The parasitic behavior of *Pedicularis palustris* on tall sedges significantly alters local plant diversity, biomass production and soil characteristics. Our experiments show that, under the right hydrological conditions and mowing management practice, several target species for nature conservation can benefit from the gaps it creates in above-ground *Carex acuta* vegetation and its dense below-ground root system. The more prominent presence of mosses and lower density of the topsoil stimulates the recovery of mesotrophic transition mire with active peat formation. Since this habitat type is specifically protected under the European Habitat Directive, (re)introduction of *Pedicularis palustris* in similar sites within its geographical distribution range in Europe may be a helpful tool to achieve the imposed obligations for appropriate management and restoration.

## Introduction

‘Ecosystem engineers’ are organisms that cause proportionally large physical state changes in the local biotic or abiotic conditions, while modulating the availability of resources to other species. In doing so they modify, maintain and create habitats. ‘Autogenic engineers’ (e.g. corals, trees) change the environment via their own physical structures (i.e. their living and dead tissues). Allogenic engineers (e.g. woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another. Simple trophic interactions and resource competition do not constitute engineering (Alper 1998; Jones et al. 1997a, 1997b). Other terms, such as ‘foundation species,’ ‘structural species’ or ‘keystone species’ are more or less analogous or show overlap with this definition (Ellison et al. 2005). Insights on the role of ecosystem engineers, either positive or negative, are currently increasingly translated into practices that aim to change the structure and function of ecosystems (e.g. Crooks 2002; Gribben et al. 2009; Hastings et al. 2007; Wright & Jones 2006). Particular focus is given to the important role of ecosystem engineers in the management, creation and restoration of ecosystems, their plant and animal communities and their functions and services (e.g. Byers et al. 2006; Crain & Bertness 2006; Gilad et al. 2004; Wright & Jones 2006).

The ‘engineering’ potential of plant species other than trees, has already been demonstrated for species, such as *Sphagnum* mosses (e.g. Rochefort 2000), tussock forming sedges (e.g. Crain & Bertness 2005), reed (e.g. Minchinton et al. 2006), specific structuring species of drylands (e.g. Coiffait-Gombault et al. 2012; Gilad et al. 2004), seagrass (e.g. van Katwijk et al. 2009) and marramgrass (e.g. Borsje et al. 2011). The hemiparasites *Rhinanthus angustifolius* and *R. minor* represent a special case. They are considered to be ecosystem engineers because of their ability to change the community structure of grassland ecosystems and several authors advocate that *Rhinanthus* spec. should be introduced as a measure for restoring species-rich semi-natural grassland (e.g. Bullock & Pywell 2005; Pywell et al. 2004). By reducing the biomass of competitive grasses on which they are parasitic, gaps are created in the grass sward which are supposed to be beneficial to the colonisation of less competitive target species. However, scientific evidence on this issue is sparse and lacks consistency. The only more or less consistent scientific result is the ability of the species to decrease the grass:forb biomass ratio. However, establishment success can be highly variable and cannot always be explained, while mixed (or only temporary) effects have been reported on the relationship with the decrease of the total

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biomass and the pursued increase of plant biodiversity (see e.g. Ameloot et al. 2005; Hellström et al. 2011 for a review of current knowledge).

Amongst hemiparasitic plant species the supposed ecosystem engineering capacity of *Rhinanthus* spec. so far represents an isolated case in current scientific literature. From accidental field observations we suspected that the rare hemiparasite *Pedicularis palustris* might behave similarly. Like Rhinanthus, *P. palustris* belongs to the family of Scrophulariacea. It is usually a biennial root hemiparasite of mesotrophic wet meadows, wet dune slacks, fens, quaking bogs and transition mires (Weeda et al. 1988). Typical host plants are both small and tall sedges (*Carex* spp.) and grasses (e.g. *Agrostis* spp., *Poa* spp., *Festuca* spp.). The species occurs in Northern, Western and Central Europe, Western and Central Siberia and Eastern Canada. In Western and Central Europe *P. palustris* has become very rare since the 1950s due to habitat loss and habitat deterioration and it is now considered a Red List species in many European countries and regions (e.g. Colling 2005; Király 2007; Ludwig & Schnittler 1996; Moser et al. 2002; Odé & Meijden 2006; Van Landuyt et al. 2006). Re-establishment of *P. palustris* in restored habitat is hampered by the fact that the species only survives in few, often small, highly fragmented and isolated populations, its short life cycle (only reproducing by seed) and the absence of a long-term persistent seed bank (Kleyer et al. 2008; Thompson et al. 1997).

In July 1987 we experimentally reintroduced *P. palustris* in our study area in the framework of a fen-meadow restoration project. The seeds originated from the most nearby population (distance: 40 km) at the 'Damvallei' (Destelbergen, 3°49′54″E–51°3′17″N). The experiment demonstrated that germination particularly occurs in sites with low productivity with a ground water table close to or at surface level during most of the year. Dry summers negatively influenced germination success. The reintroduction experiment was very successful. The population grew from 14 individuals in 1988 to more than 5000 in 1995 with densities up to 700 individuals per 100 $m^2$. All individuals in the study area are most probably descendants of only one specimen that successfully reproduced in 1988 in one of the experimental introduction plots.

During the reintroduction experiment it was very striking to observe that our study species was able to steadily invade mown, but still highly productive *Carex acuta* vegetation. In 1994 we set up an experiment to explore the effects of *P. palustris* on community development and other habitat parameters, with special attention given to effects on target fen-meadow species with conservation value.

## Methods

### Study area

Our study site is situated in the nature reserve 'Vallei van de Zuidleie' (Oostkamp) in northern Belgium (Flanders), 3°15′55″E –51°9′22″N. Due to abandonment of the traditional management of a small fen-meadow relict, the local population of *P. palustris* became extinct in the 1960s. Other parts of the area were raised with sludge from an adjacent canal. The typical fen-meadow vegetation in the untouched part shifted to wet ruderal vegetation (Filipendulion), large sedge vegetation (Magnocaricion) and expanding reed vegetation with patches of Alder carr. In 1981 a nature restoration project started and gradually small scale traditional mowing management was restored. In 1992–1994 and 2002–2006 a large restoration project removed all the sludge down to the original peaty soil surface, restoring the fen-meadow to its original size (Decleer 2008). The local soil type is peat, gradually shifting to clay on a depth of 70–90 cm. Ground water levels fluctuated most of the year around soil surface level, with a lowest level of ca. 50 cm during short, dry summer periods.

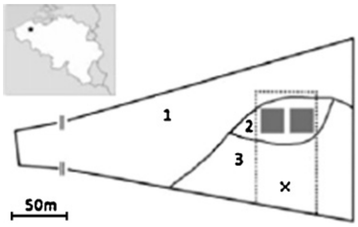

**Fig. 1.** Location of the study site in Belgium and schematic vegetation map at the start of the experiment in 1994: reed marsh and carr (1), homogenous *Carex acuta* vegetation (2), meadow invaded by *Filipendula ulmaria* and other tall herbs (3). The dotted line indicates the plot, perpendicular on the humidity gradient, where mowing management was resumed after about 30 years of spontaneous succession. The X marks the zone where *Pedicularis palustris* was reintroduced in the area in 1987. The experimental sites of 20 m × 20 m in this study are indicated as grey squares.

### Experimental set up

In the period 1994–2000 we investigated the effect of *P. palustris* on the structure and composition of a productive *Carex acuta* dominated marsh vegetation (dry biomass production in 1994: 900–1000 g $m^{-2}$). In the first phase only some tall herb species were present, such as *Filipendula ulmaria*, *Angelica sylvestris*, *Epilobium hirsutum*, *Calystegia palustris* and *Phalaris arundinacea*. In 1994 we selected two adjacent sites of 20 m × 20 m in a homogenous *Carex acuta* vegetation: one where we introduced 500 seeds of *P. palustris* in July 1994 and one control site without the hemiparasite. No other plant species were deliberately introduced. Both sites had the same mowing management regime (July and as far as possible also September), which had been resumed here in 1992. Accidental establishment of *P. palustris* in the control site was prevented by careful and accurate manual removal of young plants as soon as we detected them (especially during spring and late summer). The evolution in the number of *P. palustris* individuals in the sites with *P. palustris* 'treatment' was monitored over the period 1995–2000. Fig. 1 shows the setting of the experiment.

We evaluated the effects of *P. palustris* with the following parameters:

(1) Total and *C. acuta* biomass (July 1994, 1998 and 2000) in six randomly chosen plots of 1 m × 1 m in each site. Samples were oven dried at 40 °C and litter was excluded.
(2) Number of individuals of all plant species and moss layer cover (July 2000) in 10 randomly selected plots of 1 m × 1 m in each site. For *Agrostis stolonifera*, *Festuca rubra* and *Poa trivialis* for practical reasons only the number of flowering stalks were counted; for other species also vegetative shoots were counted as accurately as possible.
(3) Height of 30 randomly selected *C. acuta* plants in each site (July 2000), as an additional indicator for plant fitness.

Long-term trends in vegetation and soil characteristics were evaluated in June 2012 by comparing the total cover of *C. acuta* and moss layer in each site. Additionally, peat soil density was randomly sampled with an Eijkelkamp Penetrologger (30 penetrations per site, cone type 5 $cm^2$/60°, speed 2).

### Data analysis

We used a Permanova (permutational based multivariate analysis of variance) in the statistical package 'Primer 6' (Anderson 2001) to test whether after six years the species composition in the *Carex acuta* site with *P. palustris* was significantly different from the site