Reducing nutrient availability and enhancing biotic resistance limits settlement and growth of the invasive Australian swamp stonecrop (*Crassula helmsii*)

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**Abstract** The invasive Australian swamp stonecrop, *Crassula helmsii*, is a perennial amphibious herb originating from Australia and New Zealand. In freshwater wetlands of North-western Europe, this alien plant species is invasive due to its efficient colonization of empty niches. The establishment of dense *C. helmsii* growth is threatening native biodiversity and functioning of freshwater ecosystems, especially oligotrophic wetlands with high disturbance and nutrient enrichments. As the effects of these potential drivers of ecosystem degradation are generally difficult to determine in the field, we tested the competitive strength of *C. helmsii* in a greenhouse experiment with two native competitor species of the same habitat type, *Pilularia globulifera* and *Littorella uniflora*. Sods dominated by either of the native species, as well as bare soils, were collected from the field and manually infested with propagules of *C. helmsii*. Settlement and growth of *C. helmsii* was assessed after five weeks. In addition, the effect of nutrient enrichment by water bird feces on competition was studied by adding waterfowl droppings. *C. helmsii* was able to settle successfully in all treatments, but *P. globulifera* and *L. uniflora* dominance...
reduced settlement success and growth of *C. helmsii*. On vegetated sods, the addition of waterfowl droppings had a low effect on the performance of *C. helmsii*, however, this treatment significantly increased biomass production on bare soils with low nutrient availability. We conclude that both absence of native competitors and eutrophication, including guanotrophication by waterfowl, explain the establishment success and invasiveness of *C. helmsii*. Given the fact that eradication of *C. helmsii* is very challenging, our results imply that management should focus on a combination of increasing local species densities and abating eutrophication. This will strongly limit the window of opportunity for invasion of *C. helmsii* and enhance resistance by native plant communities.

**Keywords** Alien plant · Amphibious weed · Global drivers · Non-native plant · Aemi-terrestrial growth · Vegetation dominance

### Introduction

Australian swamp stonecrop *Crassula helmsii* (T.Kirk) Cockayne is a perennial amphibious plant. Native to Australia and New Zealand, this species is presumed to have been introduced to Europe for ornamental use in ponds (Dawson and Warman 1987; Robert et al. 2013). It is highly invasive in Northwestern Europe and is increasingly dominating moorlands, dune pools and other freshwater to slightly brackish wetlands, thereby threatening endangered native species and protected ecosystems (Dawson and Warman 1987; Leach and Dawson 1999; OEPP/EPPO 2007; Newman 2013; Brouwer et al. 2017; Prinz et al. 2019; Smith and Buckley 2020). Eradication of *C. helmsii* has been found to be both difficult and costly (Van der Loop et al. 2018), and effective eradication is only possible under certain conditions (Dawson and Warman 1987; Robert et al. 2013; Van Kleef et al. 2017). Only when infestations are small and isolated, and thorough measures are taken, can eradication be successful (Brouwer et al. 2017; Hussner et al. 2017; Van Kleef et al. 2017; Van der Loop et al. 2018). Since these conditions are rarely met, it is necessary to explore alternative options to control this species.

The biotic resistance of a community may reduce the success of biological invasions (e.g., Moulton and Pimm 1983; Case 1990; Kennedy et al. 2002; Levine et al. 2003). Although the mere presence of native vegetation does not enable ecosystems to resist invasions given the ongoing propagule pressure. The dominance of the invasive species can be repressed by competition (Levine et al. 2003). Furthermore, when the native vegetation has similar traits or if most available niches are occupied, new species are less likely to become established (Funk et al. 2008). Disturbances often create new available niches, which can be rapidly occupied by alien invasive species (e.g., Hobbs 1989, 1991; Hobbs and Huenneke 1992; Rejmánek 1999).

In this paper, we test the role of native species in the invasion success of *C. helmsii* in both oligo— and eutrophic ecosystems, to explore whether active management focusing on harnessing native species can reduce the settlement and dominance of *C. helmsii*. Two native species were selected, *Pilularia globulifera* L. and *Littorella uniflora* (L.) Ascherson to provide competition with *C. helmsii*. Both species occur in habitats susceptible to invasions of *C. helmsii* and are regularly found in high abundance, indicating that they may be strong competitors (e.g., Arts and Leuven 1988; Bloemendaal and Roelofs 1988). *P. globulifera* grows on soils with a relatively high organic content, whereas *L. uniflora* thrives on more oligotrophic, mineral soils. Both species form dense swards limiting space and available nutrients for *C. helmsii*, potentially affecting its settlement and growth. We therefore hypothesize that these species are able to suppress the settlement and growth of *C. helmsii* and consequently increase the biotic resistance to invasions of the alien plant species.

Additionally we study the effects of water birds on invasions of *C. helmsii*. Endo—and epizoocorous transport by water birds is believed to be an important vector for *C. helmsii*. Geese droppings contain many poorly digested plant fragments, often still capable of vegetative regeneration (Denys et al. 2014). Not only can these two processes greatly enhance propagule pressure over large areas, but nutrient release from feces also works as a natural fertilizer (Dawson and Warman 1987; Robert et al. 2013; Dean et al. 2015; Brouwer et al. 2017; Hussner et al. 2017). The enrichment of nutrients from feces is therefore hypothesized to facilitate the invasiveness of *C.
in oligotrophic ecosystems (Brouwer et al. 2017; Van Kleef et al. 2017), but only in the absence of competitors.

A greenhouse experiment was carried out to test the strength of biotic resistance exerted by native plant communities on invasive C. helmsii in oligotrophic and nutrient rich environments. An additional treatment with waterfowl feces was included to assess the potential facilitation of invasion through guanotrophication.

Materials and methods

Experimental setup

Experiments were carried out between August and November 2017 in the greenhouse facilities of Radboud University (Nijmegen, The Netherlands). Temperature was set on 20.0 and 17.1 °C during day and night, respectively. Assimilation lighting (16 h light, 8 h dark) was fixed at 174 μmol m−2 s−1. Vegetated and bare sods (26.5 × 36.5 cm) were collected from two soft water lakes in the Netherlands (i.e. Moerven and Korenburgerven). Sods containing a closed vegetation of L. uniflora and bare soils (n = 16 for each) were collected in the Moerven (nature reserve Huis ter Heide, 51°36′31.11″ N, 5°31′45.05″ E). Sods containing a closed vegetation of P. globulifera and bare soils (n = 16 for each) were collected in the Korenburgerven (nature reserve Korenburgerven, 51°59′29.87″ N, 6°38′43.91″ E). In the latter area, C. helmsii was present. Vegetated and bare ground soil composition were assumed to be equal in origin, as extractions were just a few meters apart. The sods were placed in plastic containers without draining and manually cleared from all C. helmsii biomass. Following two weeks without any new shoot formation, the sod was considered free from C. helmsii. Germination from possible seed banks in sods under experimental conditions are never recorded and features of germinating plants from seeds and sprouting from fragments, as used in this experiment, remarkably differ.

After two weeks of acclimatization to the environmental conditions of the greenhouse complex, sods were infested with C. helmsii collected from the Akkerenven (51°25′32.73″ N, 4°21′31.66″ E, The Netherlands). To simulate the settlement of C. helmsii in the field, the plant was fragmented with each plant piece containing one node and two leaves, but no roots. Hussner (2009) reported this as the minimum fragment size for regeneration. Experiments with fragments of this size mimic the dispersal of propagules by waterfowl or human assisted spread via the treat of footwear. In total, 60 C. helmsii fragments were placed within three rows with 20 fragments per sod. We used sods with bare soils (n = 30) and sods that were completely covered (100%) with L. uniflora (n = 16) or P. globulifera (n = 16).

For each treatment, half the sods received waterfowl feces which were collected in an urban and agricultural area in Arnhem (51°59′15.86″ N, 5°54′7.58″ E) and Nijmegen (51°52′44.56″ N, 5°51′49.28″ E), the Netherlands, respectively. Feces from two different species of waterfowl, Anser anser L. (Anatidae), and Alopochen aegyptiacus L. (Tadorninae), were collected in equal amounts. In order to minimize the risk of infestation by waterfowl droppings, we collected these from sites confirmed to have no C. helmsii infestation, and where waterfowl populations were predominantly sedentary birds. Before application, feces were mixed and molded in homogenous droppings of 6 gram FW (i.e. the average weight of a droppping). Nutrient content was not determined. Literature data show that geese dropping release between 371 and 500 μmol inorganic nitrogen and 40–46 mg phosphate per gram of feces (Liu et al. 2014; Frazão 2008). An amount of 6 feces was added to the duplicated sods. During the experiment approximately 13.37–18.00 mmol inorganic nitrogen and 40–46 mg phosphate per gram of feces was added. We replicated 8 sods per treatment combination, except treatment bare soils of P. globulifera with feces n = 06, for a total of 62 replicates. Table 1 shows an overview of all treatment combinations. For 8 weeks the sods were watered with rainwater every 48 h until the water level was at soil surface. Water loss only occurred by evapotranspiration. At the start of the experiment, and every two weeks thereafter, soil porewater samples were taken using rhizons. Seedlings of plant species other than L. uniflora, P. globulifera and C. helmsii, were manually removed from all sods. After 2 weeks, aphids were observed in P. globulifera vegetation, and therefore all sods were treated once with the biological control Capsanem and Entonem, nematodes Steinernema carpocapsae and S. feltiae respectively (both 0.5 million nematodes per...
m² soil surface) which successfully eradicated the aphids with no visible harm of any plant species. Settlements of *C. helmsii* propagules were counted in week 2, 5 and 8. Propagules were considered ‘settled’ when they produced new biomass such as new nodes, leaves or roots. Nine weeks after inoculation of the sods, *C. helmsii* biomass as well as soil and vegetation samples from *P. globulifera* and *L. uniflora* were harvested. One quarter of the vegetation area was harvested for analysis, and dry weights were multiplied by 4. After harvest and thorough rinsing to remove any soil particles, all plant samples were put in a drying stove for 48 h at 70 °C to determine dry weight.

### Chemical analyses

Porewater pH was measured with a standard combined glass Ag/AgCl pH electrode (Orion Research, Beverly, CA, USA) connected to a pH meter (Tim800; Radiometer analytical, Lyon, France). Alkalinity was estimated by titration to pH 4.2 with 0.1 mmol L⁻¹ HCl using an auto burette (ABU901, Radiometer, Lyon, France). An auto-analyser 3 system (Bran and Lube, Norderstedt, Germany) was used to measure concentrations of nitrate and ammonium colourimetrically using hydrazine sulphate (Kamphake et al. 1967) and salicylate (Grasshof and Johannsen 1972) respectively. An inductively coupled plasma spectrometry (ICP-OES icap 6000; ThermoFischer scientific, Waltham, MA, USA) was used to measure the concentrations of calcium, iron, magnesium, potassium, phosphorus and sulphate. Plant nitrogen content was measured by grinding dried plant material and measuring the concentration on a CN analyser (model EA NA 1500, Thermo Fisher Scientific). Soil (0.5 L) of every sod was collected and similarly analysed for its chemical content of plant available nitrogen and phosphorus content.

### Statistical analysis

Since assumptions for normality a homogeneity of variance were not met for either soil and plant chemistry, nor for *C. helmsii* response parameters, treatment effects were tested for significance using General Linear Models. Effects on settlement was tested using a quasipoisson error distribution on a log-linked GLM model, since significant overdispersion was present when using a standard Poisson error distribution. All other effect parameters were tested using a Gamma GLM with identity link. Data was tested and visualized using the statistical programme R version 3.5.2 (Team 2018). Treatment and/or treatment combination effects were tested for significance by a priori testing approach using a full factorial predictor structure (single treatment and all treatment interaction effects) in all response models. For all tested response parameter, box plots have been drawn to provide visual representation of treatment effects (Figs. 1, 2, 3, 4, 5).

### Results

#### Soil nutrient status

The Huis Ter Heide soil was characterized as nutrient poor mineral soil with low plant available inorganic nitrogen (N) and phosphorus (P) concentrations (Table 2; Fig. 1). The Korenburgerveen soil was characterized as a mineral soil substantially richer in plant available N as well as P concentration, which

### Table 1 Overview of experimental set-up with 60 *Crassula helmsii* propagules per treatment

| Treatment Code | Vegetation cover | Soil Competition | Waterfowl feces |
|----------------|------------------|------------------|-----------------|
| C+ F− 8        | L. uniflora      | Mineral          | +               |
| C+ F+ 8        | L. uniflora      | Mineral          | +               |
| C− F− 8        | Absent           | Mineral          | −               |
| C− F+ 8        | Absent           | Mineral          | +               |
| C+ F− 8        | P. globulifera   | Organic          | +               |
| C+ F+ 8        | P. globulifera   | Organic          | +               |
| C− F− 8        | Absent           | Organic          | −               |
| C− F+ 6        | Absent           | Organic          | +               |
was emphasized by a clearly visible organic layer. Average water levels of both experimental systems were 0–1 cm below soil level. Plant carbon limitation by aquatic growth was absent. Feces treatment did not significantly increase plant available P or inorganic N in the soils below the feces. Two sods (replicates of treatment combinations C–F+P. globulifera) represented significant outliers for multiple parameters, these were excluded from all statistical analysis.

**Tissue chemistry of C. helmsii**

Plant tissue N:P ratios (g/g) of *C. helmsii* strongly differed between locations after experiment. For the nutrient poor site they were 19.28 (which may be indicative of P limitation (Koerselman and Meuleman 1996; Güsewell 2004) whereas at the nutrient rich site tissue N:P ratio was 4.54 (Fig. 2). Limitations of N and P occur when ratios are ~10 and ~20, respectively. At N:P ratios between ~10 and ~20, either N or P can be limiting or plant growth is co-limited by both nutrients (Koerselman and Meuleman 1996). The addition of feces lowered N:P ratios for plants from Huis Ter Heide to 9.83, suggesting that plants became less P-limited by this treatment.

**Settlement of C. helmsii**

Settlement of *C. helmsii* on bare soils was high (83.94% of propagules), and much higher than in treatments with native plant species present (26.83%, Fig. 3, Competition: t = −4.99, p < 0.001). Nutrient status of the system had no significant effect on settlement on bare soils (Table 2; Nutrient rich: t = −0.29, p = 0.77). However, the competition effect of the native species vegetation was much stronger in the nutrient rich treatments dominated by *P. globulifera* (33.06% lower settlement) than in the nutrient poor treatments dominated by *L. uniflora* (Table 2; Competition x Nutrient rich: t = −5.40, p < 0.001).
Unexpectedly, the addition of waterfowl feces did not affect *C. helmsii* settlement, neither in the bare treatments nor in the treatments with local vegetation present (Fig. 3; Table 2). This was the case for both the nutrient rich and nutrient poor treatments (Fig. 3; Table 2).

**Biomass**

The realized biomass of *C. helmsii* was much higher on bare soil than in the presence of native plant species competition (Fig. 4, Competition: $t = -3.30$, $p < 0.01$). For the nutrient-poor and -rich site, realized biomass at the end of the experiment on bare soils was 29.9 and 281.5 times higher, respectively (Fig. 4; Table 2; Nutrient rich: $t = -2.57$, $p < 0.05$). Competition with native vegetation resulted in a strong reduction in *C. helmsii* realized biomass, indicating growth rates close to zero for both the nutrient poor and rich system (Fig. 4). As a consequence of higher realized biomass on bare soil, the competition effect was significantly stronger in nutrient rich sites (Table 2; Competition x Nutrient rich: $t = -2.60$, $p < 0.05$).

The addition of waterfowl feces only affected *C. helmsii* growth for nutrient poor, bare soil sites (Table 2; Feces: $t = 2.08$, $p < 0.05$), where realized biomass at the end of the experiment was doubled.
Growth was also stimulated for these sites when native vegetation was present (Table 2: Competition x feces: $t = -2.04, p < 0.05$). However, the absolute increase under competition was minimal compared to no competition (Fig. 2). The stimulating effect was absent in nutrient rich bare soil (Table 2: nutrient rich x feces: $t = -0.39, p = 0.7$) sods, as well as under competition in nutrient rich sods (Table 2: Competition x Nutrient rich x feces: $t = 0.38, p = 0.71$).

The total biomass of the native species was not increased by the nutrient enrichment from feces for both *L. uniflora* ($p = 0.6$) and *P. globulifera* ($p = 0.3$) (Fig. 5).

**Discussion**

Settlement of *C. helmsii* was very high on bare soils in both nutrient-rich and nutrient-poor treatments, but strongly regulated by the presence of native vegetation. In addition, competition with native species almost nullified growth of this invasive species in both systems. Although guanotrophication did not affect settlement, growth of *C. helmsii* was stimulated by bird droppings but only on bare, nutrient poor soils (Fig. 6).
Biotic resistance to invasion by the presence of native vegetation: settlement constraints

Under absence of competitors on bare soil, *C. helmsii* showed high settlement and growth rates under both nutrient poor and nutrient rich conditions. This underlines the high risk of invasiveness of *C. helmsii* in situations when native vegetation is absent or has declined, and bare soil is present. These bare conditions can be a result of natural disturbance (e.g., drought, overgrazing), but are also created by nature managers. For example, in ecological restoration projects with large-scale dredging or topsoil removal practices to re-create nutrient-poor conditions and restore biodiversity. Ecosystem disturbance leading to bare spots, both unintended and intended, therefore results in a highly increased risk of major colonization by invasive alien species in these wetlands, as reported in previous studies (Hobbs 1989, 1991; Hobbs and Huenneke 1992; Rejmánek 1999). Brouwer et al. (2017) described that the development of already settled *C. helmsii* plants on the shores of moorland pools is strongly reduced by competitors (such as *L. uniflora* and *Hypericum elodes* L.). Here, we show that a closed vegetation of *L. uniflora* in nutrient-poor, mineral systems and *P. globulifera* in more nutrient-rich, organic soil conditions strongly reduces the settlement of *C. helmsii*, supporting our hypothesis that native species strongly increase the biotic resistance to invasions of alien plant species. Settlement of new introductions is more complicated than the growth of already settled plants because of the absence of roots and thus the lagging of nutrient uptake. The settlement of *C. helmsii* was clearly suppressed under dominance of native vegetation, which resulted in the absence of open niches. Our results show that *P. globulifera* in the nutrient-richer system is better in suppressing settlement than *L. uniflora* in the more nutrient poor system. *L. uniflora* has a rosette with an open leaf canopy, resulting in a relatively open sward structure, whereas in *P. globulifera* the sward is much denser. This dense vegetation probably functions as a physical barrier for settlement, effectively withholding *C. helmsii* propagules to reach the soil with newly formed roots. Yet, since *P. globulifera* lacks winter greenness, there is still a high risk that *C. helmsii* will be able settle in winter, partially overgrowing the native vegetation, thereby cancelling out the competition gradually each year.
Biotic resistance to invasion by the presence of native vegetation: growth constraints

In addition to affecting settlement, native species have an even stronger effect on growth of *C. helmsii*. The growth of this species is reduced in the presence of competitors, with both competitors showing the capability to reduce growth to near zero growth during the experiment. As *L. uniflora* swards are markedly less dense than *P. globulifera* swards, it may be expected that this should enable *C. helmsii* to reach higher growth rates compared to the competition with *P. globulifera*. However, the root system of *L. uniflora*, occurring under nutrient-poor conditions, is very extensive and dense, and adapted to an efficient nutrient and carbon uptake (Kuntz et al. 2014; Brouwer et al. 2017), which might still have suppressed the growth of *C. helmsii* by nutrient competition due to its extensive root system. This suggests that competition for nutrients is more important than competition for space and light in explaining growth suppression under these conditions.

*P. globulifera* forms a less deep and dense root system, and is less well adapted to grow under highly oligotrophic soil conditions (Bloemendaal and Roeloys 1988). In addition, competition for nutrients is not likely under the nutrient rich soil conditions in which *P. globulifera* was grown in this experiment. Here, competition for space and light might be the causal mechanism in suppressing growth of *C. helmsii*. The nature of competition may also result from allelopathic interaction with the competitive species besides strong competition for nutrients, space and light (Rice 2012). Denton (2003) suggest that *L. uniflora* might possibly suppress *C. helmsii* by some chemical effects. However, Brouwer et al. (2007) show improved growth of *C. helmsii* when mixed with *L. uniflora*. Our results clearly indicate competition by the latter species as the most important factor. There are no indications growth restrains from allelopathic factors of *C. helmsii*. Future investigations into the role of allelopathic interactions in determining competitive strength can provide more insight in the relative importance of this factor on competition between native and invasive plant species.

Role of nutrient availability; effects of guanotrophication

For bare soil conditions, growth of *C. helmsii* was higher under nutrient rich site conditions compared to nutrient poor conditions, similar to the studies of Hussner (2009) and Brouwer et al. (2017). Plant tissue N:P ratio suggested more P-limited, or NP co-limited biomass production of *C. helmsii* at the nutrient poor treatment (Koerselman and Meuleman 1996), whereas
at the nutrient rich treatment tissue N:P ratio suggested more N-limited biomass production, similar to Brouwer et al. (2017) (Fig. 2). However, the availabilities of both N and P were much higher in the nutrient rich treatment than at the nutrient poor treatment.

Nutrient enrichment by waterfowl feces increased C. helmsii growth, but only on the bare, nutrient-poor soil. For the more nutrient-rich site, C. helmsii growth did not appear to be limited by nutrient availability, and growth suppression by P. globulifera must have been functioning via different mechanisms than by L. uniflora. The addition of feces on the bare, nutrient-poor soil sods appears to have removed P limitation or NP co-limitation. This stimulating effect by guanotrophication under nutrient poor conditions indicates that anthropogenic ecosystem disturbance at the landscape-scale has carry-over effects to nature reserves, by increasing the vulnerability of these ecosystems to invasive alien species. In the last decades, goose populations (A. anser, Anser albifrons Scopoli, Branta canadensis L., and the shelduck-sheldgoose species A. aegyptiacus, among others) have increased exponentially in the Netherlands and other parts of Europe (Larsson et al. 1988; Madsen et al. 1999; Berndt et al. 2002; Rehfisch et al. 2002; Vermeech et al. 2004; Van der Jeugd et al. 2006). Intensive land use and increased use of fertilizer increased grassland productivity, increasing overall food availability for geese (Van Eerden 1996; Fox et al. 2005; Van Eerden et al. 2005; Van der Jeugd et al. 2006). In the Netherlands, wintering geese increased by a factor of 10 between 1975 and 2014 (Van der Jeugd et al. 2006; Sovon 2015). In addition to causing eutrophication, the presence of waterfowl also increases the propagule pressure and settlement probability of C. helmsii via avian transport. Hence, increased waterfowl pressure on oligotrophic ecosystems enhances the invasiveness of C. helmsii via several mechanisms that positively influence each other. The existence of such positive feedback mechanism has also been described for other invasive alien species (e.g., Blossey and Notzold 1995; Davis 2009; Engelhardt 2011; Matzek 2011; Pasari et al. 2011) and stresses the need for policy makers to account for these landscape level interactions in nature conservancy legislation.

Implications for invasive species management

Our study shows that the presence of bare soils, functioning as empty niches, strongly creates a window of opportunity for aggressive C. helmsii colonization. In the Netherlands, these open niches often arise when former agricultural land is reclaimed for rehabilitation of nature areas. Restoration of these high production ecosystems generally takes place by removing the nutrient rich topsoil to enable the development of more biodiverse vegetation. However, when residual nutrients are retained in the system, these can facilitate the growth of C. helmsii (Dawson and Warman 1987; Dean et al. 2015; Brouwer et al. 2017; Van Kleef et al. 2017), stressing the need to maximize nutrient removal in such restoration practices. Given our findings that C. helmsii was also well able to colonize bare oligotrophic ecosystems, this can be expected to be insufficient to prevent its invasion.

We show that competition by native species vegetation highly suppresses the invasiveness of C. helmsii, suggesting that measures aimed at increasing biotic resistance of an ecosystem are likely to be effective at preventing C. helmsii dominance. Therefore, it is advisable to minimize the duration of bare soil presence after natural disturbances or as a result of management activities (Dean et al. 2015; Brouwer et al. 2017; Van Kleef et al. 2017). Given the low success levels of eradication efforts (Van der Loop et al. 2018), ecosystem-based measures focusing on low nutrient status and fast native plant recolonization, may provide a viable alternative to traditional eradication management (Van Kleef et al. 2016; Van der Loop et al. 2018). Such an approach aims at limiting settlement chance and growth conditions for C. helmsii. These measures consist of reducing nutrients on site, e.g., by removing nutrient rich top soils or limiting nutrient influx via surface water, and by the prevention of guanotrophication by water birds. A promising novel approach to boost biotic resistance is the stimulation of succession by native vegetation in newly created nature reserves or after high-disturbance nature management practices. The presence of bare soil will be limited to a shorter time frame by introducing highly competitive native plant species adapted to the specific habitat conditions (e.g., via spreading vegetative propagules or seeds). This will effectively reduce the vulnerability with respect to C. helmsii infestation. Although this prevention strategy...
does not guarantee that *C. helmsii* will not colonize the system, it may strongly hamper its invasiveness after settlement and thus reduce its ecological impact. In the Netherlands, several field experiments on cost-effectivity of system oriented management measures to increase resistance of habitats to plant invasion are currently in progress and assessments of the results will become soon available.

Most of the prevention efforts of reducing the introduction, and effects of invasive species are aimed at composing risk assessments, reducing introduction pathways and maintain an early detection and removal management.

Although these prevention strategies are important to reduce the introductions and spread of alien species, prevention can be achieved by reducing disturbances in nature areas and correct nature management as well.

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