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RESEARCH ARTICLE

The ecosystem resilience approach to control the invasive alien species Australian swamp stonecrop (*Crassula helmsii*)

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The invasive Australian swamp stonecrop (*Crassula helmsii*) threatens species characteristic of shallow soft water lakes and pools, among others, in Europe. Anthropogenic disturbances, including restoration actions, of these ecosystems cause open niches in their littoral zones and allow *C. helmsii* to form dominant stands, especially under nutrient enrichment. Eradication of this invasive alien, amphibious, and clonal plant is, however, difficult and costly once a large population has established. For this reason, we here explore an ecosystem resilience approach (ERA) to control this invasive alien species. This approach includes suppressing the species by facilitating the occurrence and expansion of native vegetation. This requires a setback of *C. helmsii*'s abundance by actively reducing its biomass, and the rehabilitation of optimal environmental conditions for native species. Our ERA study in four nature areas reveals that the introduction of native species makes the ecosystem more resilient against alien invasions, as shown by a lower abundance of this invasive plant species. Therefore, we state that ERA can effectively be applied in practice to decrease the invasibility of ecosystems by *C. helmsii*. Effectiveness, costs and benefits, and recommendations for application in practice are discussed. Overall, we argue that incorporating ERA in nature and water management will provide sustainable solutions in terms of biodiversity as well as more cost-effective applications for invasive alien species prevention and control.

Key words: amphibious weed, combating, control, non-native plant, resistance

Implications for Practice

- Facilitating the occurrence and abundance of native vegetation, and reducing anthropogenic disturbances of the ecosystems, creates an ecosystem that is more resistant against future problems with invasive species.
- The reduction of nutrients and introduction of native species by donor material can reduce the regrowth of invasive species.
- A preventive approach to invasive alien species can be combined with ecosystem resilience approach, leading to more effective restoration of ecosystems.
- The ecosystem resilience approach is an approach that is ready for application in practice and can guide restoration scientists and nature area managers in dealing with invasive species.

Introduction

Due to global trade and climate change, the number of introductions and spread of invasive species will increase (e.g. Meyerson & Mooney 2007; Hellman et al. 2008; Van Kleunen et al. 2015). With a growing number of established invasive species, their impact and costs for elimination or control will become increasingly challenging. Many invasive species prove to be resilient. Their populations quickly recover after control measures or recolonize areas where they were eradicated (e.g. Vander Zanden & Olden 2008; Simberloff 2013; Prior et al. 2018). In addition, human-induced environmental pressure has rendered ecosystems disturbed and species-poor (e.g. Vitousek et al. 1996; Sánchez-Ortiz et al. 2020), making them more vulnerable to colonization by invasive species. They often lack functional feedback mechanisms that healthy ecosystems provide, such as competition, grazing, and predation. Traditional removal of invasive species creates open niches that are also vulnerable for rapid recolonization or introduction of

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new invaders (Elton 1958; Funk et al. 2008). As a result, this traditional eradication practice is often unsuccessful (Van der Loop et al. 2018).

Undisturbed species-rich communities are less affected by invasions than disturbed species-poor communities (Hobbs & Huenneke 1992; Funk et al. 2008). By actively restoring the pristine abiotic conditions and stimulating maximum utilization of niches by native species, upcoming invasive species have little space for settlement. Hereby, dispersion barriers for native biota are nullified, as dispersal of native species to the study sites was facilitated by us, and they can make optimal use of available resources such as space, light, and nutrients (e.g. Funk et al. 2008; Thiébaut & Martinez 2015). When the native species arrive first at a site, they can significantly affect further assembly by the priority effect, including the settlement and increase of invasive species (Eriksson & Eriksson 1998; Fukami 2015). This results in much higher resistance against invasions, with minimal chance of settlement and dominance of invasive species.

The ecosystem resilience approach (ERA) is an approach to deal with invasive species that is derived from these observations. The basic concepts of this approach were already theoretically described long ago as it was broadly recognized that competition between native and invasive species is contributing as one of the most important factors to decrease invasibility of ecosystems (e.g. Crawley & May 1987; Levine & D'Antonio 1999; Bakker & Wilson 2004). Therefore, ERA is expected to reduce invasions strongly and permanently in contrast to traditional practice, decreasing both environmental damage of interventions and management costs. Dealing with invasive species is already well established as a necessary component of ecological restoration (e.g. D'Antonio & Meyerson 2002; Weidlich et al. 2020). However, as far as we know little attention has been focused on ERA in practice and a greater focus in this is needed (Guo et al. 2018).

In this study, ERA is applied in the restoration of ecosystems invaded by Australian swamp stonecrop *Crassula helmsii* (T. Kirk) Cockayn. This perennial amphibious species is expanding rapidly in Northern Europe (OEPP/EPPO 2007; Smith & Buckley 2020), threatening native species that are characteristic of shallow soft water ecosystems, among others (Dawson & Warman 1987; Smith & Buckley 2020). Eradication of *C. helmsii* is difficult because strict conditions, such as isolation and draining of the infested water bodies, must be met, as this species easily regrows back from remaining plant fragments (Van der Loop et al. 2018; Smith & Buckley 2020) and waterfowl are an important vector for (re)dispersal (Denys et al. 2014). In many cases, the effectiveness of traditional measures to control *C. helmsii* is low (e.g. Van der Loop et al. 2018; Smith & Buckley 2020).

Results of greenhouse experiments already confirm that ERA is promising for lowering the invasibility of ecosystems for *C. helmsii*. The establishment and performance of this species is strongly reduced by a high abundance of native species (Brouwer et al. 2017; Van der Loop et al. 2020). Competition for space and nutrients by a high cover of native species (e.g. *Littorella uniflora* L. and *Pillularia globulifera* L.) reduced stem fragments from settling and biomass production (Van der Loop et al. 2020). Below ground competition for nutrients by *L. uniflora* and *Hypericum elodes* L. proved to be effective to reduce growth of settled *C. helmsii* (Brouwer et al. 2017). Reducing nutrients increased the competitive strength of native species (Brouwer et al. 2017; Van der Loop et al. 2020). Evidence of competition limiting *C. helmsii* invasions has also been demonstrated in the field, where a survey of >40 sites invaded by *C. helmsii* showed that the vegetation cover and biomass of this species negatively correlated with that of native species (Van Kleef et al. 2017). These field correlations and results of greenhouse experiments need to be confirmed by field testing of ERA.

The aim of this study is to test the application of ERA in practice, to assess whether this approach is promising for reducing the invasibility in ecosystems by *C. helmsii*. The main research question to be answered is: What steps should be taken for successful introduction of competing native species after breaking the dominance of *C. helmsii* by various types of interventions (i.e. coverage with foil, sod cutting, and sod cutting with steaming). For a successful application of ERA it is important to consider costs, ecosystem impact, and availability of donor plant material. We hypothesized that the invasiveness of *C. helmsii* in nature areas could indeed be reduced by ERA and tested this hypothesis in four invaded nature areas.

Methods

Steps Required for the Application of ERA

The effectiveness of ERA in controlling invasive species is related to the occupancy degree of niches with native species that are involved in the resistance (natural defensibility) and resilience (rapid recovery) of an ecosystem (Funk et al. 2008). Optimal niche occupation after restoration depends on the physicochemical properties of an ecosystem and the arrival (priority effects) and recolonization potential of native species (e.g. Vila et al. 2011; Castro-Díez et al. 2014; Weidlich et al. 2021). Physicochemical properties of invaded ecosystems are often inadequate, for example, due to altered hydrological conditions or eutrophication. Therefore, the first step in improving ecosystem resilience is to restore abiotic properties inherent to undisturbed situation (Van Kleef et al. 2017). In addition, the recolonization potential of native species is often impaired by ecosystem disturbance and population fragmentation, resulting in poor metapopulations of native species in situ. The subsequent dominance of invasive species has led their scarcity or local extinction. Therefore, in the second step recolonization of native species—in particular, species that are able to compete with the invasive species—is artificially stimulated by replenishing their numbers. However, prior to this reintroduction of native species, it is necessary to reduce the biomass of *C. helmsii* once, to decrease its dominance and to enhance reestablishment of introduced native species. Methods used include covering vegetation with foil, sod cutting, and a hot water treatment, but these methods alone are not effective for sustainable control of *C. helmsii* (Van der Loop et al. 2018). Next, native plant species are introduced to stimulate competition and to reduce resettlement and regrowth of *C. helmsii*. Native species may fill open niches and reduce the available resources. Depending on the growth characteristics of the target species, seeds, root fragments, and entire plants can be used for introduction. The suitability of native species is context-dependent and varies with the frequency of inundation, soil conditions, and desired management objectives of the area (Van Kleef et al. 2017).

Cases

The effectiveness of ERA against *C. helmsii* was tested in four nature areas in the Netherlands, namely Doorbraak, Huis Ter Heide, Reten, and Plateaux (Fig. 1, Supplement S1). These sites differ in ecological characteristics and are therefore described separately. Measures to restore the abiotic conditions at the sites were previously carried out by nature managers. The areas were severely infested by *C. helmsii*, resulting in a 100% coverage over large areas.

Doorbraak. The watercourse “Doorbraak” is located in a nature area near the municipality of Almelo in the Netherlands (52°20′22.30″N/6°42′28.21″O; Fig. 1). This water system has a length of 13 km and the downstream part is located in the nature reserve Mokkelengoor (52°19′14.00″N/6°36′18.13″O). This nature reserve (44 ha) in a low-lying part of the Pleistocene cover sand area is part of the protected Netherlands Nature Network and is characterized by the presence of remote moorland pools. The hydrology and abiotic conditions of Doorbraak were restored in 2015 and the area currently fulfills an important water storage and drainage function. However, soil disturbances during its restoration, occasional flooding with nutrient rich water, and intensive grazing by livestock left the banks vulnerable to *C. helmsii* invasion (Van Kleef & Van der Loop 2021).

In August 2018, two sites (in the south and the north) were fenced to prevent livestock from entering these areas and to allow undisturbed vegetation development. However, inflow of nutrient rich water could not be stopped because the drainage function of the watercourse needed to be ensured for the safety against flooding of nearby inhabited areas. After fencing of both locations, the topsoil (approximately 10 cm deep) with a dominant coverage (>80%) of *C. helmsii* was removed to break its dominance. On the northern location 16 and the southern

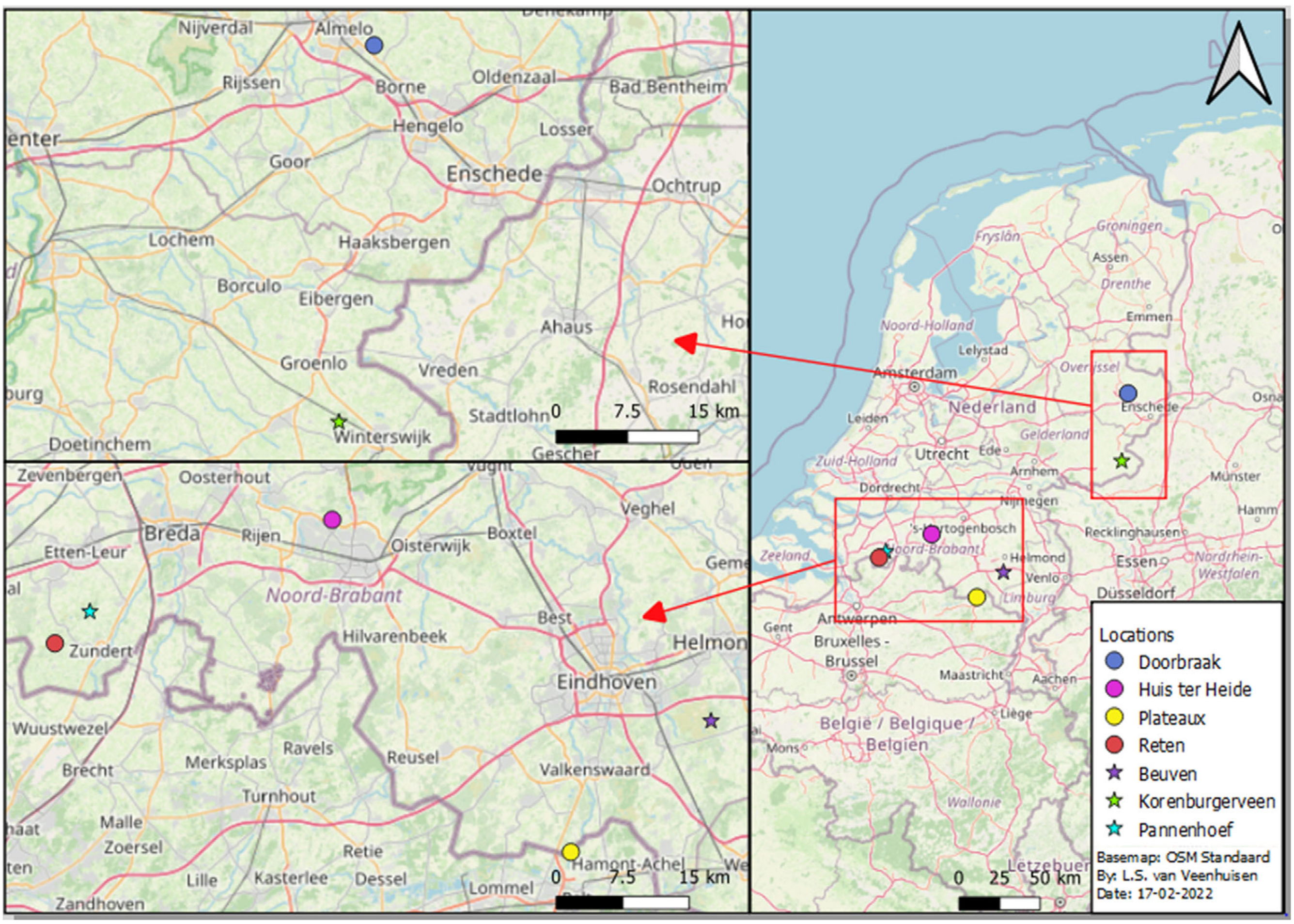

Figure 1. Locations of the nature areas where the ecosystem resilience approach against *Crassula helmsii* was applied (◦) and locations where donor plant material was collected (☆).

location 10 plots of 4 × 4 m were laid out (Table 1). In the southern location, five plots were randomly selected for stimulating the colonization of native species. In September 2018, approximately 0.05 m^3 of clippings, containing plant fragments and seeds, obtained from species rich wet meadows in the nearby nature reserve Mokkelengoor were spread over 1 m^2 of planting area. This vegetation was chosen because it suits the site characteristics and desired species development of the area. The other five plots served as a control and were left untreated.

The northern plots were located slightly higher on the bank of Doorbraak and considered more suitable for the development of a drier grassland type. Here, eight plots that were randomly selected for native species stimulation received a total of 5.08 g seeds/m^2 planting area, from a commercial flower grassland mixture for year-round wet to moist, nutrient-rich soils (Cruydt Hoeck G3 mixture; see Supplement S2). Again eight control plots remained untreated. The seed mixture contained only native species and 50% of this mixture consisted of grassland species (Supplement S2). Before sowing, the soil was roughened slightly with a rake. Sowing was done twice: in September 2018 and April 2019.

Huis Ter Heide. The nature area "Huis Ter Heide" is located in the municipality of Tilburg (51°36′05.92″N/5°02′06.66″O; Fig. 1). This area is characterized by a heterogeneous landscape of heathland, forests, and moorland pools. In 2009, the nutrient-poor abiotic conditions were restored by excavating the former agricultural area and new heathland pools were created. These ponds became quickly infested by *C. helmsii* (cover >99%). Nature managers used different methods to eradicate or control *C. helmsii*, that is, removal by hand and machines, placing foil for 5 years, and a dye treatment in one of the pools (1.23 ha) (Denys et al. 2014). None of these attempts was successful (Van der Loop et al. 2018).

In this area two locations were selected. One location was on the southern bank of a newly created moorland pool. The second location was a shallow depression between two pools (Vossenbergven 1 and 2) that was naturally inundated several months every year (approximately November–March). At both locations, black polyvinyl chloride (PVC) foil (thickness 0.5 mm) was placed in order to block sunlight and to smother and break dominance of *C. helmsii*. After 2.5 years, in June 2017, the foil was removed and at each location 20 plots (4 × 4 m) were marked (Fig. S1). From each set of 20 plots, 10 were randomly selected for stimulation of native species. Ten plots on each location were left untreated to serve as control. On both locations, 0.016 m^3 *L. uniflora* was introduced per square meter planting area. This species is abundant in other moorland pools in the area with similar characteristics and could therefore be easily collected and used. Free floating plants were collected in a nearby moorland pool "Leikeven" (51°36′25.72″N/5°01′58.40″O). Before spreading the plants, the soil was roughened slightly with a rake to facilitate rooting.

Reten. Nature reserve "Reten" is located in the municipality Zundert in the Netherlands (51°28′39.55″N/4°35′12.44″O; Fig. S1) and is characterized by grasslands, heather, and moorland pools. In the years 2008–2009, the former agricultural area was transformed into an ecological corridor between the nature areas Moeren (21°29′00.14″N/4°37′13.92″O) and Oude Buisse Heide (51°28′26.97″N/4°33′47.96″O). During this restoration project, several new moorland pools were dug. Although during the project about 40 cm of the nutrient rich topsoil was removed, the remaining soil was still enriched with phosphate.

The experimental setup in de Reten differed slightly from that in the other areas because we intended to test in practice which measure best reduced the biomass of *C. helmsii*. On the bank of a moorland pool, three sets of 20 plot areas were selected. In these plots, *C. helmsii* biomass was reduced by: (1) covering with PVC foil (thickness 0.5 mm) for 1.5 years, (2) 15 cm deep topsoil removal, and (3) 15 cm deep topsoil removal followed by a hot water treatment (>98°C) using a steam lance (Table 1). At each location, 20 plots (4 × 4 m) were marked of which 10 plots were randomly selected for stimulation of native species and 10 were left untreated as control. After reducing the biomass of *C. helmsii*, the plots were planted with a mixture of three different plant species: *Eleogiton fluitans* (L.) Link, *Hypericum elodes* L., and *Pilularia globulifera* L., with a density of 190, 190, and 125 cm^3/m^2 planting area, respectively. *E. fluitans* and *H. elodes* were collected from Pannenhoef (51°30′32.06″N/4°38′13.46″O), and *P. globulifera* from Korenburgerven (51°59′04.68″N/6°40′03.84″O). Because the locations were never overgrown with vegetation other than *C. helmsii*, and there are no comparable, uncontaminated water systems nearby, these species were chosen by expert judgment and tested to determine their competitiveness against the invasive species.

Plateaux. Nature area "Plateaux" is located in the municipality of Bergeijk (51°16′01.03″N/5°25′10.22″E) near the Belgian border (Fig. S1) and is part of the Natura 2000 site "Leenderbos, Groote Heide, & De Plateaux." This nature area lies between dry sandy soils and the valley of the river Dommel. At the end of the last millennium much effort was put in the restoration and construction of poorly buffered moorland pools on former agricultural soils. The nutrient-enriched top layers were removed. In the following years, the area was invaded by *C. helmsii*. On the bank of a heavily invaded pool 1000 m^2 PVC foil (thickness 0.5 mm) was placed in 2017 to break *C. helmsii*'s dominance. After 1.5 years, in June 2019, the foil was removed and parallel to the shore two sets of 20 plots (4× 4 m) were marked. From each set of 20 plots, 10 plots were randomly selected for stimulation of native species. Ten plots on each location were left untreated to serve as control. In the plots highest on the bank clippings (0.038 m^3/m^2 planting area), containing plant fragments and seeds, were spread in September 2019. These clippings were collected from moist heathland within the reserve. On the selected plots closest to the waterline, *L. uniflora* was introduced with a density of 0.016 m^3 plants/m^2 planting area and *Baldellia ranunculoides* ssp. *ranunculoides* L., 0.33 g of seeds/m^2 planting area. Species were chosen because of their availability and matching site characteristics. The free-floating

Table 1. Experimental setup for the application of the ecosystem resilience approach to control *Crassula helmsii* in four cases. Statistical significance of effects of various treatments on coverage and diversity of native plant species and relative reduction (%) of *C. helmsii* in 10 treatment and 10 control plots. NA: not applicable. Green: positive outcome after treatment; red: negative outcome after treatment.

Treatment			*Effects on Plant Coverage*			*Effects on the Number of Native Plant Species Present*	*Relative Reduction of* C. helmsii		
Area	*Measures to Reduce* C. helmsii *Biomass in Plots of 4 × 4 m* (n = 20)	*Introduced native plant species in half* (n = 10) *of the plots*	*Inhibition of* C. helmsii	*Successful establishment of introduced plant native species (coverage)*	*Successful establishment of native plant species by natural succession (coverage)*	*Higher number of native plant species present*	C. helmsii *regrowth in treated areas (%)*	C. helmsii *regrowth in untreated areas (%)*	*Relative reduction of* C. helmsii *(%) in the treated areas (%)*
Doorbraak (duration 3 years)									
South	Sod cutting ($n = 10$ plots)	Clippings	Significant ($p = 0.03$)	Significant ($p = 0.03$)	NA	Significant ($p = 0.01$)	34.0	69.8	51.3
North	Sod cutting ($n = 16$ plots)	Commercial seed mixture	Significant ($p = 0.01$)	Significant ($p < 0.01$)	Significant ($p = 0.05$)	Significant ($p \leq 0.01$)	18.9	41.9	54.9
Huis Ter Heide (duration 3 years)									
Bank of moorland pool	Cover with foil	*Littorella uniflora*	Significant ($p = 0.01$)	Significant ($p < 0.01$)	Significant ($p = 0.03$)	Not significant ($p = 0.23$)	6.9	15.5	55.5
Bank of inundation site	Cover with foil	*L. uniflora*	Not significant ($p = 0.84$)	Significant ($p \leq 0.01$)	Not significant ($p = 0.13$)	Not significant ($p = 0.97$)	1.1	0.7	−59.2
Reten (duration 2 years)									
South	Cover with foil	*Eleogiton fluitans*, *Hypericum elodes*, and *Pilularia globulifera*	Not significant ($p = 0.45$)	Not significant ($p = 0.82$)	Not significant ($p = 0.44$)	Not significant ($p = 0.88$)	2.6	1.5	−82.1
West	Sod cutting	*E. fluitans*, *H. elodes*, and *P. globulifera*	Not significant ($p = 0.54$)	Significant ($p \leq 0.01$)	Significant ($p \leq 0.01$)	Not significant ($p = 0.44$)	2.6	2.8	6.8
North	Sod cutting + hot water ($n = 21$)	*E. fluitans*, *H. elodes*, and *P. globulifera*	Not significant ($p = 0.11$)	Significant ($p = 0.01$)	Significant ($p \leq 0.01$)	Not significant ($p = 0.07$)	0.2	0.7	70.2
Plateaux (duration 3 years)									
Bank	Cover with foil	Clippings	Not significant ($p = 0.97$)	Not significant ($p = 0.71$)	NA	NA	47.9	46.8	−2.4
Shoreline	Cover with foil	*L. uniflora*	Significant ($p \leq 0.00$)	Significant ($p \leq 0.01$)	Not significant ($p = 0.90$)	NA	37.0	79.5	53.5

L. uniflora plants were collected in the nearby Beuven (51°24′10.34″N/5°38′45.38″E). *B. ranunculoides* ssp. *ranunculoides* was obtained locally from "Plateaux." Prior to spreading of the plants, the soil was roughened slightly with a rake to facilitate rooting.

Effect Measurement

The effects of reducing the biomass of *C. helmsii* and introducing native plant species on plant coverage were determined by recording the coverage (%) and number of plant species after 3 years in Doorbraak, Huis Ter Heide, and Plateaux, and after 2 years in Reten. Data of treated sites were compared with control sites (Table 1). In addition, based on our experiences during the implementation of the measures, we qualitatively assessed large-scale applicability, labor intensity, costs, impacts on the ecosystem, pros and cons of various ERA treatments of the measures (Table 2).

Statistics

All data were tested and visualized using the statistical program R version 4.0.4 (R Core Team 2021). When normality assumptions were met, the Student's t test was used, to test for treatment effects between treated and untreated groups for *C. helmsii* coverage, native species coverage, introduced native plant coverage, and the number of native species. If normality assumptions were not met, a nonparametric Wilcoxon-signed rank test was used to test for these treatment effects.

Table 2. Comparison between different components of the ecosystem resilience approach treatments.

	Effectivity	*Large-Scale Applicability*	*Labor Intensity*	*Costs*	*Impact on the Ecosystem*	*Pros*	*Cons*
Crassula helmsii reduction							
Foil	High	Medium	Medium	Medium	Medium	No disposal of soil material Seed bank native species still present	Unaesthetic when foil is present Long execution (>2 years)
Sod cutting	High	Medium	Medium	Medium	High	Fast execution	Disposal of soil material can be difficult Entering the area with heavy machinery
Sod cutting combined with hot water	High	Low	High	High	High		Disposal of soil material can be difficult Unknown effects on biodiversity in soil Entering the area with heavy machinery Only to be performed when site is not inundated
Vegetation for *C. helmsii* suppression							
Clippings	Variable	High	Low	Low	Low	Easy to obtain	Washes away easily with rising water levels
Commercial seed mixture	Low	High	Low	Medium	Low	Easy to obtain	Possible presence of unwanted species
Littorella uniflora	High	Medium	Medium	Low (obtaining plants from donor sites / High (cultivating local plant material)	Low	Easy establishment in wet periods	Only applicable with suitable climate conditions, only available from limited number of sites and only after storms
Combination of *Eleogiton fluitans, Hypericum elodes*, and *Pilularia globulifera*	NA	Low	High	Medium (obtaining plants from donor sites) High (cultivating local plant material)	Low		Difficult establishment Only applicable with suitable climate conditions

To find statistically significant differences in *C. helmsii* coverage, native species coverage, introduced native plant coverage, and the number of native species between the three tested methods (foil, sod cutting, and sod cutting with additional hot water treatment) in the Reten area, a linear model analysis of variance was used when normality assumptions were met and a Kruskal–Wallis test was used if normality assumptions were not met.

Results

Doorbraak

Clipping Treatment: Southern Plots. The treatment where native plant species were sowed via clippings with plant fragments and seeds had a significant effect on the mean coverage of herbs, grasses (and other native plant species; Table 1; Fig. 2; $t = -2.60$, $p = 0.03$), with a higher coverage (%) of plants in introduced treatment plots (see Table S1 for the complete dataset). *Bryophyta* did slightly better in plots where clippings were introduced. *Juncus articulatus* L. had the highest average coverage (4.8%), indicating that this species significantly benefited from the clipping addition. In addition, some other species had a higher abundance in the clipping treatment (i.e. *Molinia caerulea* L., *Plantago lanceolate* L., *Pinguicula vulgaris* L., and *Sphagnum denticulatum* L.). However, the coverage of these species was low (<1%) after two growing seasons. The control plots did not harbor native species with high abundance. *Isolepis setacea* L. R.Br. had a relatively higher presence, but negligible coverage (<1%). *C. helmsii* was the only species with high abundance (average 69.8%) after two growth seasons in the control plots. Coverage of *C. helmsii* was significantly lower in the grass clippings plots ($t = 2.66$, $p = 0.03$). As vegetation cover had not yet closed, growth of *C. helmsii* increased but interaction with the introduced native species resulted in a lower coverage of this invasive species. The introduction of clippings also had a positive effect on species richness of the southern trial areas ($t = -3.27$, $p = 0.01$).

Seed Mixture Treatment: Northern Plots. In the sown plots in the northern location, various grasses (average coverage of *Cynosurus cristatus* L. 8.9%, *Anthoxanthum odoratum* L. 4.4%, among others) and herbs (average coverage of *Lotus pedunculatus* L. 21%, *Trifolium repens* L. 6.8%, among others) were the dominant species (Tables 1 & S2; Fig. 3). Fourteen of the 27 sown species were observed in the plots with a significantly higher coverage compared to control plots ($W = 1$, $p < 0.01$).

Coverage of native species, other than the introduced species, was higher in control plots, whereas cover of introduced species was highest in treatment plots ($t = -2.19$, $p = 0.046$). In control plots, the number of species with high abundance was much lower. These species concern *Bryum* species and *T. repens* with 44 and 13.9% coverage, respectively.

Crassula helmsii increased rapidly in coverage, reaching 41.9% mean coverage after 2 years in the control plots. In the treatment plots, this species also increased (to 18.9%), but coverage is significantly less ($t = 2.91$, $p = 0.01$). In the treated plots, the average species richness after two growing seasons was lower than in the control plots ($t = 4.57$, $p = 0.01$).

Huis Ter Heide

Moorland Pool. Plots on the banks of the moorland pool in which *L. uniflora* was introduced had a significantly lower coverage of *C. helmsii* compared to untreated plots ($t = 3.93$, $p < 0.01$; Tables 1 & S3; Fig. 4). Plots with introduced vegetation show that *L. uniflora* has a significantly higher cover (bank $W = 89$, $p < 0.01$; Table S4).

Several native plant species colonized the location resulting in natural vegetation succession. However, total coverages of native species, such as *Lythrum portula* (L.) D.A. Webb and *Elatine hexandra* (Lapierre) DC., were significantly lower in the treatment plots with *L. uniflora* on banks of the moorland pool ($W = 0.88$, $p = 0.03$) than in control plots. The average number of species, including *L. uniflora*, did not significantly differ between plots where native vegetation was sowed and untreated control plots ($t = -1.23$, $p = 0.23$).

Inundation Site. Only a few plants of *C. helmsii* recolonized plots in the inundation site with both treatments and no significant effect was seen ($W = 46.50$, $p = 0.84$; Table 1; Fig. 4). The plots with introduced vegetation show that *L. uniflora* has a significantly higher cover (bank inundation site $W = -4.29$, $p \leq 0.01$; Table S4). The treatment plots at the inundation site and the control plots do not differ in total cover of naturally established species ($t = 1.59$, $p = 0.13$). The average number of species, including *L. uniflora*, did not significantly differ between plots where native vegetation was sowed and untreated control plots ($t = -0.04$, $p = 0.97$).

Reten

Effectiveness of Biomass Reduction Methods. Recolonization of *C. helmsii* significantly differed between plots with different methods for biomass reduction. Plots in which the coverage of *C. helmsii* was reduced by sod cutting combined with a hot water treatment showed lower recolonization of *C. helmsii* than plots where biomass was reduced by foil or sod cutting, but differences were small (recolonization 0.6, 2.1, and 2.7%, respectively) (Tables 1, S5–S7; Fig. 5, $\chi^2 = 10.66$, $p < 0.01$). The establishment of the vegetation of sowed species is independent of these methods. However, for plants that establish naturally, the foil treatment is the most favorable in comparison to the sod cuttings with or without hot water treatment ($F = 31.88$, $p \leq 0.01$).

The number of recolonizing native species was higher in the set of plots where biomass of *C. helmsii* was reduced by covering with foil ($F = 30.89$, $p \leq 0.01$) compared to sod cuttings with or without hot water treatment. The plots in which the biomass of *C. helmsii* was reduced by means of sod cutting had a higher plant diversity than the treatments with hot water ($F = 30.42$, $p < 0.01$).

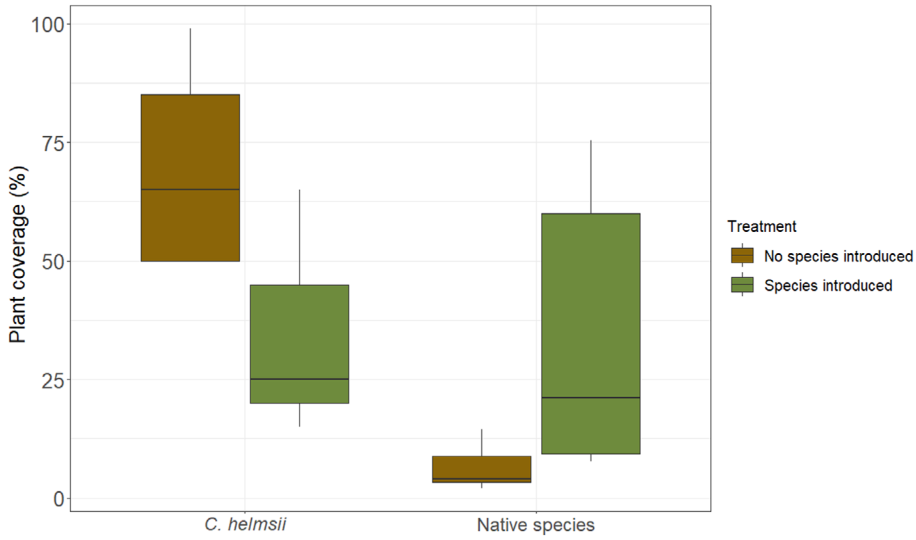

Figure 2. Coverage after 3 years of *Crassula helmsii* and native plant species in plots where clippings of native meadow species were spread ($n = 5$) and unsowed ($n = 5$) plots at the southern location of Doorbraak. The boxplot displays the first quartile, median, and third quartile (box lines), and minimum and maximum values.

Vegetation Development. For the plots treated with foil, after 1.5 years, the *C. helmsii* coverage is on average 2.0%, which is considerably lower than the situation outside the plots, where its coverage is 100%. The introduction of native plant species has not inhibited the recolonization of *C. helmsii* (Tables 1, S5–S7; Fig. 5). There are no differences in coverage of *C. helmsii* between plots with or without introduction of native plant species ($W = 40$, $p = 0.45$). Coverages of *C. helmsii*, introduced species and species established through natural colonization were still low at the end of this project.

There is no significant difference between coverage of the introduced species ($W = 53.5$, $p = 0.82$) and total coverage of naturally established species ($t = -0.79$, $p = 0.44$) compared to the control areas without species introductions and where biomass was reduced with foil. The total number of species present (including introduced species) does not differ between treatments with or without the introduction of native plant species ($t = -0.16$, $p = 0.88$).

For the location where *C. helmsii* was reduced by sod cutting, *C. helmsii* growth was lower compared to the control plots, but no effect of introductions of native species on coverage of

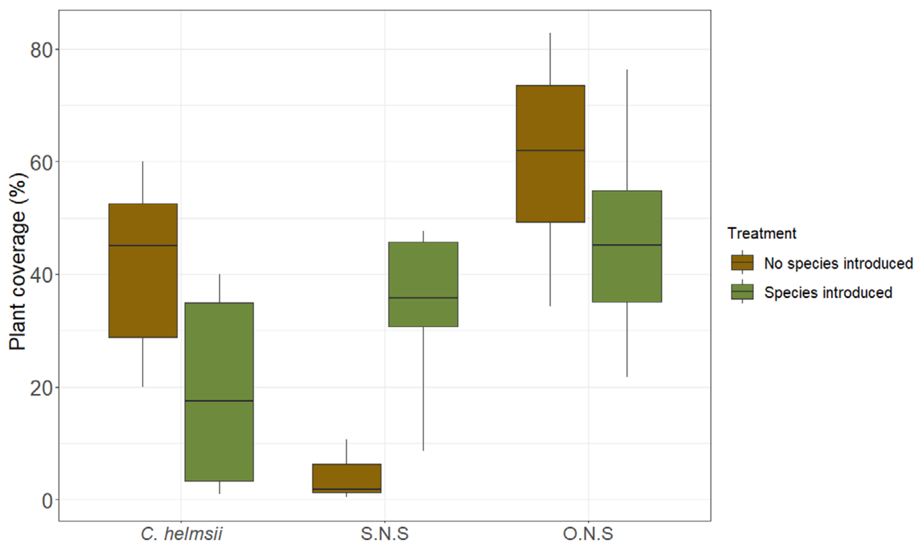

Figure 3. Coverage after 3 years of *Crassula helmsii*, sowed native plant species (SNS, including naturally established species that are similar to introduced species) and naturally established native plant species (other native species [ONS]) in sowed ($n = 5$) and unsowed ($n = 5$) plots at the northern location of Doorbraak. The boxplot displays the first quartile, median, and third quartile (box lines), and minimum and maximum values.

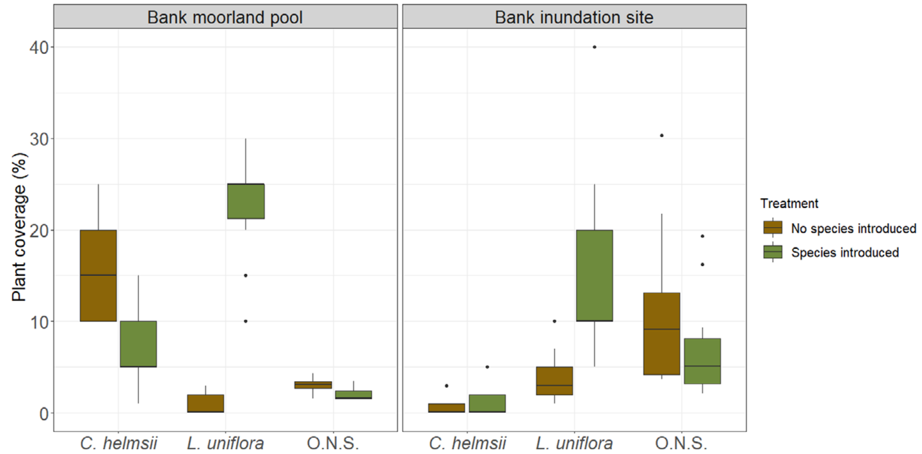

Figure 4. Coverage after 3 years of *Crassula helmsii*, *Littorella uniflora*, and naturally established native plant species (other native species [ONS]) in plots where species *L. uniflora* (sowed $n = 10$) was added and unsowed ($n = 10$) plots at the two locations of Huis Ter Heide. The boxplot displays the first quartile, median, and third quartile (box lines), and minimum and maximum values.

C. helmsii was observed (Tables 1, S5–S7; Fig. 5; $W = 58.5$, $p = 0.54$). There was, a significant difference in coverage of the plant species compared to plots where no plants were introduced ($W = 0$, $p \leq 0.01$). This was also the case for the total coverage with native species in plots with or without introduction of native plants ($t = -6.81$, $p \leq 0.01$).

Sod cutting in combination with a hot water treatment, as with the other methods, results in strong reduction of *C. helmsii* coverage. The introduction of native plant species (coverage 5%) had no effect on the recolonization of *C. helmsii* (Table 1; Fig. 5; $W = 75.5$, $p = 0.11$). However, coverage of sowed native species, as with sod cutting alone, was higher compared to the control areas where no native plants were introduced ($W = 9$, $p < 0.01$). This is also the case for total coverage with native species in plots with and without introduction of plants ($t = -4.21$, $p \leq 0.01$). There was no significant difference in the number of plant species between sowed plots with sod cutting only ($p = 0.44$) or for sod cutting in combination with the hot water treatment ($t = -1.89$, $p = 0.07$).

Plateaux

Sowing Treatment: Lower Bank. In Plateaux, only vegetation coverage of *C. helmsii*, *L. uniflora*, *B. ranunculoides* ssp. *ranunculoides* and the total coverage of native species was measured. In spring 2020, the growth of introduced *L. uniflora* plants in Plateaux took off well despite dry and relatively unfavorable conditions under which they were sowed in 2019. *C. helmsii* had significantly less coverage ($t = 7.71$, $p < 0.01$), and *L. uniflora* significantly more ($W = 0$, $p \leq 0.01$) in plots sowed with this native species compared to control plots (Tables 1 & S8; Fig. 6). There was no significant difference in establishment

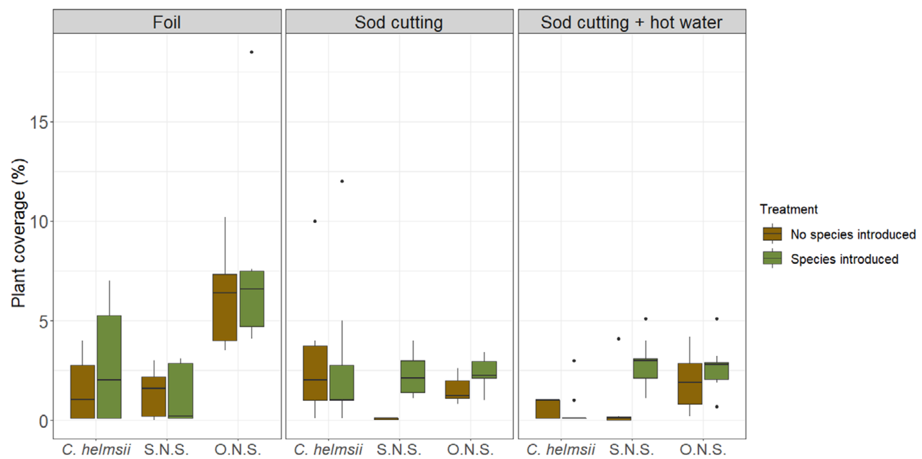

Figure 5. Coverage after 2 years of *Crassula helmsii*, sowed native species (SNS) and naturally established native plant species (other native species [ONS]) in plots where *Eleogiton fluitans*, *Hypericum elodes* and *Pilularia globulifera* were sowed ($n = 10$) and unsowed ($n = 10$) plots at the Reten with various treatments for biomass reduction of *C. helmsii* (coverage with foil, sod cutting and sod cutting with additional hot water treatment). The boxplot displays the first quartile, median and third quartile (box lines), and minimum and maximum values.

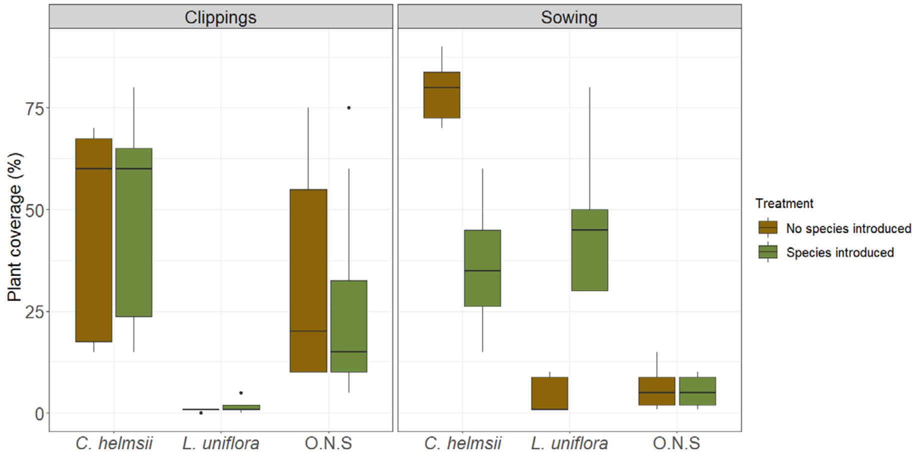

Figure 6. Coverage after 3 years of clippings (left) or *Crassula helmsii*, *Littorella uniflora* (right) or naturally established native plant species (other native species [ONS]) in plots where *L. uniflora* or clippings (treated) were added ($n = 10$) and unsowed ($n = 10$) plots at the two locations of Plateaux. The boxplot displays the first quartile, median, and third quartile (box lines), and minimum and maximum values.

of native vegetation and the seeds of *B. ranunculoides* ssp. *ranunculoides* between the treatment and control plots ($W = 51.5$, $p = 0.94$).

Clipping Treatment: Higher Bank. The introduction of clippings with plant fragments and seeds had no significant effect on coverage of *C. helmsii* ($W = 66.5$, $p = 1.00$), *L. uniflora* ($W = 46$, $p = 0.12$) and coverage of other native vegetation (Tables 1 & S9; Fig. 6; $W = 72$, $p = 0.73$). See Table 2 for the comparisons between the different components of the treatments.

Discussion

Data Considerations

As this innovative approach for *Crassula helmsii* has only been performed in four nature areas, all with site specific characteristics and treatments, it is difficult to draw generic conclusions about the minimal required coverage of native species to actively suppress *C. helmsii*. More implementations of this approach will yield data for development of a more standardized application. However, the best method for biomass reduction of *C. helmsii* and the most suitable native species for competition are always context dependent and should be selected based on an assessment of location specific characteristics. We here show that making an ecosystem more resilient against invasions of *C. helmsii* by restoring abiotic conditions, a reduction of its biomass and introduction of native species, is an ERA that can be applied in practice to control this invasive species. In this study, the sowing of native vegetation was found to be effective in most cases to suppress biomass increase of recolonizing *C. helmsii*.

ERA in Practice

Reducing Nutrients. The study areas were recently reconstructed and the nutrient-rich top layer had already been removed in all of them for the benefit of nature restoration. This means that a more nutrient poor condition had already been established. In addition, livestock was removed from all experimental sites. This is beneficial for reducing nutrients and preventing disturbance due to trampling of the areas and to prevent the spread of *C. helmsii* fragments. The sod cuttings in the sites Doorbraak and Reten were only executed to break the dominance of *C. helmsii* and were limited to removing the organic top layer.

Creating Open Niches. Covering with foil and sod cutting with and without a hot water treatment reduced the coverage of *C. helmsii* in all cases with more than 95% compared to the baseline situation, outside the plots which still had a 100% cover of *C. helmsii* on 12 March 2022 (J. van der Loop, personal observation). Sod cutting and foil application were both effective, whereas hot water treatment only improved the results with a few percentages. Therefore, this expensive and labor-intensive method is not preferred over the cheaper and easier to perform foil or sod cutting treatment.

Although additional sod cutting, after removal of the nutrient rich layer (restoration measure), is the fastest way to reduce *C. helmsii*, the coverage with sowed native species after 2 years is higher in treatments where *C. helmsii* is reduced by using foil. This may be explained by the fact that under the foil there are still roots, tubers, and seeds of native vegetation, and microorganisms necessary for growth, while these were scraped off with sod cutting. Restoration of native vegetation progresses faster in locations where foil was used to create open niches for the establishment of native species, whereas regrowth of *C. helmsii* was equally low in both treatments. The use of foil also has other advantages, such as keeping the soil structure intact, not having to dispose soil material, and being relatively cheap. In case of a nutrient-rich and organic layer under the dense *C. helmsii* vegetation, the use of a foil is expected to be less effective because of a more severe recolonization of *C. helmsii* facilitated by the high nutrient availability resulting from decomposing plant material after this intervention. Additionally, the treatment with foil must be applied for at least 2 years, which ensures a long duration of the treatment, and can only be applied to terrestrial areas that only are incidentally inundated because otherwise the foil may float away.

Stimulating Competition. The coverage of *C. helmsii* in Doorbraak was inhibited 23–36% by the introduction of native plant species through clippings or seeds. Due to differences in habitat conditions (especially wetness) between the two locations, it is impossible to assess which treatment is better for inhibiting growth of *C. helmsii*. On the banks of Plateaux, the introduction of clippings did not suppress *C. helmsii*. The clippings were partly blown and washed away by the wind and high water levels. These processes mimic the natural disturbance of this type of ecosystem. Although the species richness of native vegetation at this location was higher than in the plots where only *L. uniflora* was applied, the abundance was still too low to suppress *C. helmsii*.

The introduction of seeds in Doorbraak led to a high coverage of some species, that is, *Cynosurus cristatus* L., *Anthoxanthum odoratum* L., and *Lotus pedunculatus* Cav. The habitat conditions appeared unsuitable for some of the sown species, that is, *Poa pratensis* L., *Ajuga reptans* L., and *Angelica sylvestris* L., resulting in only a small proportion of introduced species managing to establish and expand. Therefore, there was no positive effect on species richness. However, a rapid increase of the vegetation coverage and thereby reducing the area with bare soil, from seeds still resulted in inhibition of *C. helmsii*'s recolonization. This argues for stimulating high trait redundancy by introducing many species; in this way there is always enough establishment of species to compete with the invasive species (e.g. Funk et al. 2008; Thiébaut & Martinez 2015; Castro-Díez et al. 2016).

The introduction of *L. uniflora* resulted in successful establishment and high cover of this species in Huis Ter Heide and Plateaux. This inhibited recolonization of *C. helmsii*. On the banks of the moorland pool in Huis Ter Heide, the growth of *C. helmsii* in the treated plots is lower than in untreated plots, but still relatively high. The reason is that *C. helmsii* washes up from the water layer, resulting in a very high propagule pressure. Nevertheless, even with this high propagule pressure, *C. helmsii* is still inhibited by the presence of *L. uniflora*. On the banks of Plateaux, there is no difference between natural succession of native vegetation in treated and untreated plots.

On the banks of the inundation site of Huis Ter Heide, propagule pressure was lower as the regrowth of *C. helmsii* only occurred from plant parts that survived the foil treatment or recolonized the plots from neighboring populations. In these plots regrowth of the invasive species is low. Coverage of naturally established native species increased strongly at this location, indicating that creating open niches also gave native species the opportunity to establish themselves in an area that was previously completely dominantly covered by *C. helmsii*.

Introduction of *Eleogiton fluitans*, *Hypericum elodes*, and *Pilularia globulifera* did not result in a coverage of native vegetation that sufficiently suppressed the recolonization of *C. helmsii*. The introduced vegetation successfully established, as species were still present in the plots, but was not competitive enough to reduce the regrowth of *C. helmsii*. The invasive species was not inhibited by competition effects after introducing a combination of these native species. Since the overall plant cover was very low during the last measurements of the experiment, it was possibly too early to observe interactions between the species. It is unknown whether coverage of native vegetation will further increase on the long run and therefore it is important to assess the effectiveness of ERA in long-term field experiments as well.

Effectivity of ERA

Overall, we show that ERA can indeed be successful to reduce the recolonization of *C. helmsii* and preventing the invasive species from becoming the dominant species in the ecosystem. Whether the approach will also be a sustainable application on the long run, and whether native species withstand, the ongoing regrowth of the invader over time, remains to be evaluated in long-term monitoring programs. It is also not clear what the long-term expectations are, under the influence of varying weather conditions partly resulting from climate change. The deterioration of abiotic conditions over time resulting from ERA-interventions may also be a relevant issue for further research.

Application of ERA rehabilitated the ecosystems conditions (i.e. abundance of native species and abiotic properties). The initial removal of the nutrient rich layer, removal of *C. helmsii*, and reintroduction of native species resulted in ecosystem recovery and increase of biotic resistance against invader dominance in situations where native species have settled well. In this case, the dominant cover of *C. helmsii* was transformed into a sward dominated by native species that are characteristic of the habitat types in the study sites. Because the vegetation does not completely cover the plots, the remaining bare soil still gives room for the establishment of other native species dispersing from surrounding nature areas that are not infested by *C. helmsii*.

ERA appeared unsuitable for the complete eradication of *C. helmsii*. This species is still present on all test locations after ERA measures, although being suppressed at lower abundance for at least 3 years. Therefore, it is expected to have less negative effects on native species. Further research will show the development of the plant diversity on the long term.

Embedding in Other Global Studies

Competition between native and invasive species is generally regarded as one of the most important factors to decrease invasibility of ecosystems. Increasing the biotic resistance of the ecosystem native species can limit the invasion of other species (Elton 1958; Crawley & May 1987; Bakker & Wilson 2004). It is a fact that many researches were already performed to prove these statements, both in theoretical studies and small-scale experiments (e.g. Kennedy et al. 2002; Chadwell & Engelhardt 2008; Thiébaut & Martinez 2015). However, full-scale restoration of disturbed and invaded ecosystems followed by measures for increasing native species community to control invasive species has only been applied to a very limited extent (Byun & Lee 2017), even though this approach is mentioned as an opportunity to develop restoration strategies after biological invasions (e.g. Shea & Chesson 2002; Zedler 2005; Funk et al. 2008). In practice, invasive species are mostly managed by eradication or population control of invaders, to minimize their impact on biodiversity and functioning of ecosystems (e.g. Simberloff 2005; Castro-Díez et al. 2016). Eradication attempts for alien invaders are often frivolous and their removal may also have unforeseen consequences (D'Antonio & Meyerson 2002; Van der Loop et al. 2018). Management strategies should, in addition, pay more attention to novel approaches for increasing ecosystem resistance and resilience (e.g. Elmqvist et al. 2003; Bakker & Wilson 2004; Denslow 2007). In fact, when ERA is used for the prevention of invasions or reducing dominance of invaders, it probably is the most cost-effective method (Westbrooks & Eplee 2011; Byun & Lee 2017). This approach has not yet been carried out in full extent for *C. helmsii*, but the results of the limited applications of ERA to control other invasive species are consistent. Increasing competition by native species consistently reduced the growth of invasive *Phragmites australis* (Cav.) Trin. ex Steud. in a tidal marsh (Peter & Burdick 2010), and the dominance of *Reynoutria japonica* (Houtt.) Ronse Decr. was effectively suppressed by adding native species mixtures (Skinner et al. 2012). Recolonization by *Phalaris arundinacea* L. was limited by altering light and soil nitrogen, reducing propagule pressure, and introducing *Carex hystericina* Muhl. ex Willd. These were all experimental studies but aimed at controlling the invasive species in practice (Perry et al. 2004; Iannone III & Galatowitsch 2008). For *Eichhornia crassipes* (Mart.) Solms in a river delta it was shown that its cover was decreased by facilitating submerged aquatic plant species cover (Khanna et al. 2012). Sowing seeds of native species can increase biotic resistance to invasions of *Agropyron cristatum* (L.) Gaertn. in the northern Great Plains of North America (Bakker & Wilson 2004). However, we expect that there will be more unreported and ongoing cases on ERA in practice.

Restoration and Prevention in Invaded Ecosystems

Inclusion ERA in restoration measures has many advantages over eradication and traditional control of invasive species. Inclusion of this approach means that that measures do not need to be repeated, have less impact on the ecosystem, facilitate colonization by native species, and decrease disturbance by preventing recolonization by invasive plants (Simmons 2005; Khanna et al. 2012). Reintroduction of native plant communities is an alternative, preferred method to protect ecosystems against impacts of invasive plants (Seabloom et al. 2003; Byun & Lee 2017). Moreover, restoring ecosystems before invasive species become abundant can reduce the magnitude of the invasion (Bakker & Wilson 2004). We think, however, that the ERA is not only applicable in systems that are already invaded but can also serve as a method of prevention of uninfested areas against future invasions. Native species that are introduced after disturbances of the ecosystem establish first can significantly affect ecosystem structure (e.g. Funk et al. 2008; Fukami 2015; Weidlich et al. 2020, 2021). This priority effect can form a barrier against invasive alien species becoming dominant (Eriksson & Eriksson 1998; Fukami 2015).

Implementation of the Study

The results of this study are promising as we show that it is indeed possible to limit the presence of *C. helmsii* by combining traditional control measured with active revegetation. Introducing native species could be an issue of debate for nature managers, as they may prefer to rely on natural succession to reestablish native plant communities after eradication of invasive species. However, insufficient native propagule pressure combined with legacy effects of invasive plant species generally means that passive approaches to restoration are often inadequate to establish native communities and prevent reinvasion (Schuster et al. 2018). The alternative ERA approach requires additional efforts such as raising awareness and bringing this topic into the scientific and societal debate of acting against invasive species.

Careful consideration should be given to which native species should be introduced considering the ecosystem properties, management objectives, and applicable (country specific) legislation regarding species introduction. In fact, control of invasive species by ERA through the elimination of disturbance and introduction of native species is a component of restoration ecology approaches (e.g. Young 2000; Palmer et al. 2016), with the addition that biological invasions require a faster intervention to recover or create biotic resistance because of problems caused by recolonization of invasive species. Obtaining the desired donor vegetation can be difficult, especially for large-scale applications. Suitable areas with large donor populations should not be infested with invasive species and must be in close distance in order to maintain region specific genetic diversity of plants and to limit the introduction of diseases. Next, the donor area should not become vulnerable to invasive species after harvesting of plant material. An alternative for the use of donor populations is to cultivate plants, using a small number of individuals of the target species.

Introducing plant species can be challenging as each species has its own specific habitat preferences. The introduced vegetation will not likely establish enough to suppress an invader when the environmental conditions are not optimal. This study was focused on the application of ERA on semi-terrestrial areas. Application of ERA under submerged conditions will probably be more challenging due to technical problems with planting, for instance because of poor transparency of the water in some systems, which hinders vision while working, and the drifting of the introduced plants, among others. We expect a low effectiveness of ERA in naturally eutrophic areas, as biomass of *C. helmsii* rapidly increases and suppresses the establishment and growth of native species (Brouwer et al. 2017; Van der Loop et al. 2020). This highlights the need for improving the habitat quality in ERA.

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LITERATURE CITED

Bakker JD, Wilson SD (2004) Using ecological restoration to constrain biological invasion. Journal of Applied Ecology 41:1058–1064. https://doi.org/10.1111/j.0021-8901.2004.00962.x

Brouwer E, Denys L, Lucassen ECHET, Buiks M, Onkelinx T (2017) Competitive strength of Australian swamp stonecrop (*Crassula helmsii*) invading moorland pools. Aquatic Invasions 12:321–331. https://doi.org/10.3391/ai.2017.12.3.06

Byun C, Lee EJ (2017) Ecological application of biotic resistance to control the invasion of an invasive plant, *Ageratina altissima*. Ecology and Evolution 7:2181–2192. https://doi.org/10.1002/ece3.2799

Castro-Díez P, Godoy O, Alonso A, Gallardo A, Saldana A (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. Ecology Letters 17:1–12. https://doi.org/10.1111/ele.12197

Castro-Díez P, Pauchard A, Traveset A, Vil M (2016) Linking the impacts of plant invasion on community functional structure and ecosystem properties. Journal of Vegetation Science 27:1233–1242. https://doi.org/10.1111/jvs.12429

Chadwell TB, Engelhardt KA (2008) Effects of pre-existing submersed vegetation and propagule pressure on the invasion success of *Hydrilla verticillata*. Journal of Applied Ecology 45:515–523. https://doi.org/10.1111/j.1365-2664.2007.01384.x

Crawley MJ, May RM (1987) Population dynamics and plant community structure: competition between annuals and perrenials. Journal of Theoretical Biology 125:475–489. https://doi.org/10.1016/S0022-5193(87)80215-1

D'Antonio CM, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restoration Ecology 10:703–713. https://doi.org/10.1046/j.1526-100X.2002.01051.x

Dawson F, Warman E (1987) *Crassula helmsii* (T. Kirk) Cockayne: is it an aggressive alien aquatic plant in Britain? Biological Conservation 42:247–272. https://doi.org/10.1016/0006-3207(87)90071-1

Denslow J (2007) Managing dominance of invasive plants in wildlands. Current Science 93:1579–1586

Denys L, Packet J, Jambon W, Scheers K (2014) Dispersal of the non-native invasive species *Crassula helmsii* (Crassulaceae) may involve seeds and endozoochorous transport by birds. New Journal of Botany 4:104–106. https://doi.org/10.1179/2042349714Y.0000000046

Elmqvist T, Folke C, Nyström M, Peterson G, Bengtsson J, Walker B, Norberg J (2003) Response diversity, ecosystem change, and resilience. Frontiers in Ecology and the Environment 1:488–494. https://doi.org/10.1890/1540-9295(2003)001[0488:RDECAR]2.0.CO;2

Elton CS (1958) The ecology of invasions by animals and plants. Methuen and Co Ltd., London, United Kingdom. https://doi.org/10.1007/978-1-4899-7214-9

Eriksson O, Eriksson Å (1998) Effects of arrival order and seed size on germination of grassland plants: are there assembly rules during recruitment? Ecological Research 13:229–239. https://doi.org/10.1046/j.1440-1703.1998.00260.x

Fukami T (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. Annual Review of Ecology, Evolution, and Systematics 46:1–23. https://doi.org/10.1146/annurev-ecolsys-110411-160340

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution 23:695–703. https://doi.org/10.1016/j.tree.2008.07.013

Guo Q, Brockway DG, Larson DL, Wang D, Ren H (2018) Improving ecological restoration to curb biotic invasion—a practical guide. Invasive Plant Science and Management 11:163–174. https://doi.org/10.1017/inp.2018.29

Hellman JJ, Byers JE, Bierwagen BG, Dukes JS (2008) Five potential consequences of climate change for invasive species. Conservation Biology 22:534–543. https://doi.org/10.1111/j.1523-1739.2008.00951.x

Hobbs J, Huenneke F (1992) Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324–337. https://doi.org/10.1046/j.1523-1739.1992.06030324.x

Iannone BV III, Galatowitsch SM (2008) Altering light and soil N to limit *Phalaris arundinacea* reinvasion in sedge meadow restoration. Restoration Ecology 16:689–701. https://doi.org/10.1111/j.1526-100X.2008.00481.x

Kennedy TA, Naeem S, Howe KM, Knops JM, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638. https://doi.org/10.1038/nature00776

Khanna S, Santos MJ, Hestir EL, Ustin SL (2012) Plant community dynamics relative to the changing distribution of a highly invasive species, *Eichornia crassipes*: a remote sensing perspective. Biological Invasions 14:717–733. https://doi.org/10.1007/s10530-011-0112-x

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26. https://doi.org/10.2307/3546992

Meyerson LA, Mooney HA (2007) Invasive alien species in an era of globalization. Frontiers in Ecology and the Environment 5:199–208. https://doi.org/10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2

OEPP/EPPO (2007) Data sheets on quarantine pests. *Crassula helmsii*. Bulletin OEPP/EPPO Bulletin 37:225–229

Palmer MA, Zedler JB, Falk DA (2016) Pages 3–26. Foundations of restoration ecology. Island Press, Washington D.C.

Perry LG, Galatowitsch SM, Rosen CJ (2004) Competitive control of invasive vegetation: a native wetland sedge suppresses *Phalaris arundinacea* in carbon-enriched soil. Journal of Applied Ecology 41:151–162. https://doi.org/10.1111/j.1365-2664.2004.00871.x

Peter CR, Burdick DM (2010) Can plant competition and diversity reduce the growth and survival of exotic *Phragmites australis* invading a tidal marsh? Estuaries and Coasts 33:1225–1236. https://doi.org/10.1007/s12237-010-9328-8

Prior KM, Adams DC, Klepzig KD, Hulcr J (2018) When does invasive species removal lead to ecological recovery? Implications for management success. Biological Invasions 20:267–283. https://doi.org/10.1007/s10530-017-1542-x

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org (accessed 7 Feb 2022)

Sánchez-Ortiz K, Taylor KJM, De Palma A, Essl F, Dawson W, Kreft H, et al. (2020) Effects of land-use change and related pressures on alien and native subsets of island communities. PLoS One 15:1–19. https://doi.org/10.1371/journal.pone.0227169

Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. Journal of Applied Ecology 55:2362–2373. https://doi.org/10.1111/1365-2664.13195

Seabloom EW, Borer ET, Boucher VL, Burton RS, Cottingham KL, Goldwasser L, Gram WK, Kendall BE, Micheli F (2003) Competition, seed limitation, disturbance, and reestablishment of California native annual forbs. Ecological Applications 13:575–592. https://doi.org/10.1890/1051-0761(2003)013[0575:CSLDAR]2.0.CO;2

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17:170–176. https://doi.org/10.1016/S0169-5347(02)02495-3

Simberloff D (2005) Non-native species do threaten the natural environment! Journal of Agricultural and Environmental Ethics 18:595–607. https://doi.org/10.1007/s10806-005-2851-0

Simberloff D (2013) Invasive species: what everyone needs to know. Oxford University Press, New York. https://doi.org/10.1093/wentk/9780199922017.001.0001

Simmons MT (2005) Bullying the bullies: the selective control of an exotic, invasive annual (*Rapistrum rugosum*) by oversowing with a competitive native species (*Gaillardia pulchella*). Restoration Ecology 13:609–615. https://doi.org/10.1111/j.1526-100X.2005.00078.x

Skinner RH, van der Grinten M, Gover AE (2012) Planting native species to control site reinfestation by Japanese knotweed (*Fallopia japonica*). Ecological Restoration 30:192–199. https://doi.org/10.3368/er.30.3.192

Smith T, Buckley P (2020) Biological flora of the British Isles: *Crassula helmsii*. Journal of Ecology 108:797–813. https://doi.org/10.1111/1365-2745.13336

Thiébaut G, Martinez L (2015) An exotic macrophyte bed may facilitate the anchorage of exotic propagules during the first stage of invasion. Hydrobiologia 746:183–196. https://doi.org/10.1007/s10750-014-1982-6

Van der Loop JMM, de Hoop L, van Kleef HH, Leuven RSEW (2018) Effectiveness of eradication measures for the invasive Australian swamp stonecrop *Crassula helmsii*. Management of Biological Invasions 9:343–355. https://doi.org/10.3391/mbi.2018.9.3.16

Van der Loop JMM, Tjampens J, Vogels JJ, van Kleef HH, Lamers LP, Leuven RSEW (2020) Reducing nutrient availability and enhancing biotic resistance limits settlement and growth of the invasive Australian swamp stonecrop (*Crassula helmsii*). Biological Invasions 22:3391–3402. https://doi.org/10.1007/s10530-020-02327-0

Van Kleef HH, Brouwer E, Van der Loop JMM, Buiks M, Lucassen ECHET (2017) Systeemgerichte bestrijding van watercrassula. Report of the Bargerveen Foundation, Nijmegen, The Netherlands (in Dutch)

Van Kleef HH, Van der Loop JMM (2021) Pilot watercrassulabeheer in de Doorbraak. Report of the Bargerveen Foundation, Nijmegen, The Netherlands (in Dutch)

Van Kleunen M, Dawson W, Essl F, Pergl J, Winter M, Weber E, et al. (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. https://doi.org/10.1038/nature14910

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. Canadian Journal of Fisheries and Aquatic Sciences 65:1512–1522. https://doi.org/10.1139/F08-099

Vila M, Espinar JL, Hejda M, Hulme PE, Jarosik V, Maron JL, Pergl J, Schaffner U, Sun Y, Pysek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14:702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. American Scientist 84:468–478

Weidlich EWA, Flórido FG, Sorrini TB, Brancalion PHS (2020) Controlling invasive plant species in ecological restoration: a global review. Journal of Applied Ecology 57:1806–1817. https://doi.org/10.1111/1365-2664.13656

Weidlich EWA, Nelson CR, Maron JL, Callaway RM, Delory BM, Temperton VM (2021) Priority effects and ecological restoration. Restoration Ecology 29:e13317. https://doi.org/10.1111/rec.13317

Westbrooks RG, Eplee RE (2011) Early detection and rapid response. In: Encyclopedia of biological invasions. University of California Press, Berkeley, California

Young TP (2000) Restoration ecology and conservation biology. Biological Conservation 92:73–83. https://doi.org/10.1016/S0006-3207(99)00057-9

Zedler J (2005) Ecological restoration: guidance from theory. San Francisco Estuary and Watershed Science 3:1–31. https://doi.org/10.15447/sfews.2005v3iss2art4

Supporting Information

The following information may be found in the online version of this article:

Supplement S1. Characteristics of the different nature areas.
Supplement S2. Native species in the Cruydt Hoeck, G3 mixture.
Figure S1. Photo impression of the experimental setup for testing the ecosystem resilience approach against *Crassula helmsii* on the banks of the moorland pool in the nature area Huis Ter Heide.
Table S1. Plant coverage (%) and number of plant species at the southern location in De Doorbraak (30 September 2021).
Table S2. Plant coverage (%) and number of plant species at the northern location in De Doorbraak (30 September 2021).
Table S3. Plant coverage (%) and number of plant species at the bank site location in Huis Ter Heide (9 October 2020).
Table S4. Plant coverage (%) and number of plant species at the inundation site in Huis Ter Heide (9 October 2020).
Table S5. Plant coverage (%) and number of plant species in the foil plots in De Reten (13 October 2020).
Table S6. Plant coverage (%) and number of plant species in the sod cutting plots in De Reten (13 October 2020).
Table S7. Plant coverage (%) and number of plant species in the sod cutting and hot water plots in De Reten (13 October 2020).
Table S8. Plant coverage (%) at the sowing treatment site in De Plateaux (19 October 2020).
Table S9. Plant coverage (%) at the clipping treatment site in De Plateaux (19 October 2020).

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