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Grazing Vertebrates Promote Invasive Swamp Stonecrop (*Crassula helmsii*) Abundance

Clare E. Dean, John Day, Rodolphe E. Gozlan, and Anita Diaz*

The macrophyte swamp stonecrop has invaded a wide range of wetland habitats across Europe. An experiment was conducted within an invaded fen habitat, which tested whether the presence of grazing disturbance affected the relative abundance of swamp stonecrop, and whether any detected effect was suppressive or facilitative. The abundance of swamp stonecrop and co-occurring resident plants was monitored within fenced grazing exclosures and in adjacent unfenced plots. Swamp stonecrop abundance was higher in the unfenced plots compared to the fenced exclosures ($t_{(87)} = 28.974$, $P < 0.001$), whereas the abundance of co-occurring plants was higher in the fenced exclosures compared to the unfenced plots ($t_{(87)} = 6.264$, $P < 0.001$). These results indicate that the presence of large vertebrates could facilitate a higher abundance of swamp stonecrop in situations where competitive resident plant species were selectively removed by these grazing animals.

Nomenclature: Swamp stonecrop, *Crassula helmsii* (Kirk) Cockayne.

Key words: Grazing disturbance, grazing exclosures, plant community dominance, removal of plant competitors.

The effect of grazing disturbance on plant community structure is variable, dependent on the intensity and the type of grazing animal, as well as the individual response of plant species to this form of disturbance (Bakker et al. 2006; Bullock et al. 2001; Milchunas et al. 1988; Olff and Ritchie 1998). However, it is generally recognized that grazing disturbance can directly affect the composition of plant communities by altering the survival and biomass of individual species, and can indirectly affect the composition by altering plant–plant interactions (Crawley 1997; Huston 2004; Olff and Ritchie 1998). It is therefore possible that the intensity of grazing within a habitat can influence the extent to which a nonnative plant produces dominating invasive growth, both by directly affecting the invader, and by mediating the abundance and competitive strength of co-occurring plant species (Mitchell et al. 2006).

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The invasive nonnative species Australian swamp stonecrop (*Crassula helmsii* (Kirk) Cockayne; sometimes known as Australian swamp stonecrop or New Zealand pygmy weed) is a perennial evergreen forb. *C. helmsii* typically occupies the margins and shallows of water bodies, where it produces prostrate and creeping stems that spread across the ground. It can also form dense stands of erect stems up to 100 mm (4 in) tall (CAPM 2004; Dawson and Warman 1987; EPPO 2007; Preston and Croft 1997). *C. helmsii* is native to southern Australia and New Zealand, but has invaded many countries in western Europe, including the U.K. (EPPO 2007; Minchin 2008), and has been recorded in North Carolina, Florida, and Washington in the United States (USDA 2014). This species can tolerate water chemistry from acid to alkaline, from low to high nutrient levels, and from freshwater to slightly brackish conditions (Dean et al. 2013; EPPO 2007; Preston and Croft 1997), and therefore can invade a wide range of wetland habitats.

C. helmsii can form extensive mats of vegetation across the marginal and emergent zones of water bodies, and in some locations, these mats grow to become extremely dense, with few or no other plants occurring among the invasive vegetation. There are concerns that such vigorous growth could be indicative of a competitively dominant species, and that the dense mats of *C. helmsii* can smother small plants and suppress their growth (Dawson and Warman 1987). Conservationists suggest that *C. helmsii*

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Management Implications

It is important to understand the efficacy of management practices designed to increase native plant diversity in communities that have been invaded by a nonnative invasive plant. The results from this study suggest that in fen habitats, disturbance from vertebrate grazing animals along drawdown zones facilitates the development of high Australian swamp stonecrop (*Crassula helmsii* (Kirk) Cockayne) abundance. If replications of this experimental design produce concurrent results, it could be concluded that wetland habitat grazed by livestock is particularly vulnerable to *C. helmsii* colonization and the extensive spread of this species. It would therefore follow that land managers of such habitat should enforce biosecurity measures to reduce the likelihood of *C. helmsii* propagules being introduced, and should invest time into frequently checking grazed drawdown zones for colonizing *C. helmsii* and act quickly to eliminate any that is found. It is advisable to prevent grazing livestock access to drawdown zones where *C. helmsii* already occurs, or in areas near to where *C. helmsii* occurs, in order to limit *C. helmsii* plant community dominance. Such actions would, however, present a dilemma for land managers, who would otherwise use livestock to create patches of vegetation with an open structure in order to encourage native plant species that require this type of microhabitat.

invasion can reduce the abundance of native vegetation, and could potentially exclude specific wetland species (Bridge 2005; Gomes 2005; Wilton-Jones 2005), reducing diversity. By extension, there are concerns that the development of dense *C. helmsii* mats could negatively affect other organisms in the ecosystem by displacing plant species which other organisms rely on, reducing the availability of bare ground and open water, or by locally depleting dissolved oxygen levels in water bodies (CAPM 2004; Foster 2010; Langdon et al. 2004; Watson 1999). Aside from the concerns regarding the ecological impacts of *C. helmsii*, this species is not part of the desired species assemblage for which wetland nature reserves are managed in Europe and North America. Also, because *C. helmsii* is classed as an invasive nonnative species, land managers are encouraged to take action to control it (Environment Agency 2010), using resources (funding, equipment, labor) (Williams et al. 2010) which could have been used for other conservation activities.

Because *C. helmsii* occurs in habitats that use livestock grazing as a management tool (for example, fens and grazing meadows; Preston and Croft 1997); it is important to investigate how this invasive nonnative plant responds to disturbance created by large vertebrates. In particular, does the presence of grazing livestock influence whether *C. helmsii* forms dense, dominating vegetative mats? Light grazing by livestock, such as cattle and sheep, is used in the management of fen habitat to encourage plant species diversity by suppressing the abundance of tall, highly competitive and dominating plant species. This suppression can occur both via consumption of biomass, and via vegetative damage from trampling (McBride et al. 2011; Natural England 2005). It can be hypothesized that because *C helmsii* is a plant species that can produce extensive aboveground biomass, the presence of grazing animals could limit its overall abundance through consumption or trampling degradation. Grazing could therefore offer a way of limiting the dominance of this invasive species in fen habitat. However, this hypothesis is predicated on the assumption that *C. helmsii* would be selected by grazing animals or that it would be suppressed by trampling, and furthermore, that it would experience more negative impacts from grazing disturbance than other plant species in the community. In fact, studies of other invasive plants and ecosystems have shown that grazing can sometimes facilitate dominance by a nonnative invasive species, if that species is less negatively affected by grazing disturbance than the native competitors (Hille Ris Lambers et al. 2010; Kimball and Schiffman 2003; Stahlherber and D'Antonio 2013).

The aim of this study was to test if the presence of grazing disturbance affected the relative abundance of *C. helmsii* within a plant community, and if so, whether grazing had a suppressive or facilitative effect on *C. helmsii* abundance. The benefits of this study were thus twofold: (1) it offered insight into whether grazing disturbance is an ecological factor that can mediate dominating invasive *C. helmsii* growth, and (2) it offered an assessment of whether livestock grazing is an appropriate management technique for maintaining higher plant species diversity in *C. helmsii*-invaded habitats. To address this aim, a field experiment was conducted in which grazing exclosures were set up along a heavily *C. helmsii*-invaded lake drawdown zone, in a fen habitat where livestock grazing was used as a management tool to limit the abundance of tall, dominating herbaceous species. The abundance of *C. hemsii* and the co-occurring plant community was monitored in these exclosures, and was compared with control plots that were accessible to large vertebrates. Three questions were asked: (1) Is there an effect of grazing disturbance on the abundance of *C. helmsii*? (2) Is there an effect of grazing disturbance on the abundance and species diversity of co-occurring vegetation? and (3) Is there an effect of grazing disturbance on species dominance?

Materials and Methods

Study Area. The experiment was sited at Kingfishers Bridge, a privately owned nature reserve in Cambridgeshire, U.K. (OS grid reference: TL 540 732). This nature reserve contains a freshwater lake with a variable marginal habitat of reed beds and open patches of shorter vegetation, and a water meadow with drainage ditches. The lake and its margins provide a suitable habitat for wild birds, including waterfowl. This reserve is also one of the few locations in

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the U.K. where water germander (*Teucrium scordium* L.) is known to occur. It is a nationally rare forb that is classified as "endangered" according to the International Union for Conservation of Nature (IUCN) Red List definition (Cheffings and Farrell 2005; JNCC 2010). *T. scordium* occurs in fen habitat, within shallow water and in wet areas adjacent to water (Beecroft et al. 2007), and therefore its habitat preferences overlap with those of *C. helmsii*. In July 2012, the pH of the water in the lake was recorded to range between pH 7.4 and 9.1. Available nutrient levels were relatively high, ranging between 1.500 and 1.700 mg L^{-1} (0.0002 oz gal^{-1}) nitrate; 0.035 and 1.040 mg L^{-1} ammonia + ammonium; and 0.150 and 0.548 mg L^{-1} total phosphorus (unpublished data). Initial detection of *C. helmsii* at this nature reserve was in 2007, along the drawdown zone of the lake (C. J. Cadbury, personal communication). During the data collection period of the experiment *C. helmsii* occurred along this drawdown zone at high abundance, forming a dense mat of vegetation.

Experimental Setup and Data Collection. Six grazing exclosures were set up along a wide section of the drawdown zone, on the southern margin of the lake where *C. helmsii* was growing in abundance. These exclosures were 4 m^2 (43 ft^2) in area with 1 m- (3 ft 3 in-) high fencing, and designed to impede access by medium to large vertebrates. The exclosures were set up on February 28, 2012, pre-empting spring vegetation regeneration; at this point the drawdown zone where the exclosures were located was predominantly bare ground with scattered patches of *C. helmsii* which had persisted through the winter. At the same time, the positions of six grazed (unfenced) 2-m^2 plots were designated, interspersed within the grazing exclosures but separated by a buffer zone of 1 m, and located so that all plots experienced water levels of an equivalent depth.

Grazing pressure and livestock type varied during the experiment based on the habitat management decisions of the reserve warden: sheep were grazed from January to March 2012 and from August 2012 to October 2013, and 11 buffalo were grazed from late July to December 2012. The site was also frequently visited throughout the year by herbivorous wildfowl. This variation meant that *C. helmsii* response to grazing intensity could not be ascertained, and this experiment purely focuses on the response of *C. helmsii* to the presence or absence of vertebrate grazing.

The plots were surveyed eight times between July 2012 and October 2013, with a 2-mo gap between each subsequent survey. The first survey was conducted on July 16, 2012 to coincide with the end of the ground-nesting bird season and the presence of seasonal vegetation growth. The final survey was conducted on October 4, 2013, coinciding with the end of the main growing season. In each plot, the abundance of *C. helmsii* was recorded as an estimate of percentage cover. All co-occurring plants were identified to species level using standard keys for vascular plants (Rose 1989, 2006), and the percentage cover was estimated separately for each species. The maximum height of vegetation was recorded throughout the experiment, and the maximum height of *C. helmsii* specifically was recorded during the last four surveys of the experiment, as an added line of enquiry.

Statistical Analysis. Before analysis, all percentage cover data were arcsine-transformed, utilizing the formula:

$$= \mathrm{DEGREES}\left\{\mathrm{ASIN}\left[\mathrm{SQRT}(\text{'abundance'}/100)\right]\right\} \quad [1]$$

in which DEGREES converts radians to degrees, ASIN is the inverse sine, SQRT is the square root, and 'abundance' is the percentage cover of a particular plant species (Dytham 2011). These transformations were conducted in Excel 2010 (Microsoft Corp.).

The effect of grazing disturbance on *C. helmsii* abundance (question 1) was assessed using a linear mixed-effects model, with the R package "nlme" (Pinheiro et al. 2013) in R version 3.0.2 (The R Foundation for Statistical Computing). The transformed data from all eight surveys were included in a linear model to test for an effect of "grazing treatment" on *C. helmsii* abundance. The variable "survey" was included as a random factor in this model in order to account for the nonindependence of data collected from the same plots over the eight survey dates.

To investigate the effect of grazing disturbance on the abundance and species diversity of co-occurring vegetation (question 2), values for the abundance of co-occurring vegetation, and species diversity, per plot per survey, were first calculated. The abundance of co-occurring vegetation was calculated as the sum of the cover of all plant species recorded within a plot on a particular survey date, excluding *C. helmsii*. All vegetation percentage cover data were arcsine-transformed before analysis. To quantify plant species diversity in each plot, the Shannon-Weiner diversity index (H) was calculated in Excel 2010 (Microsoft Corp.), using the equation:

$$\mathrm{H} = -\Sigma\left[\mathrm{P_i}\log(\mathrm{P_i})\right] \quad [2]$$

Where P_i is the proportion of an individual species relative to total vegetation cover, and log is the natural log (Begon et al. 2002). Again, this variable excluded *C. helmsii*. Abundance and species diversity were tested separately for an effect of grazing, using data from all eight surveys, in linear mixed effects models with "survey" included as a random factor.

To investigate the effect of grazing disturbance on species dominance (question 3), it first had to be ascertained which plant species recorded within the survey were the most dominant. Dominance was scored based on

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proportional abundance, defined as the abundance of a plant species relative to the total amount of vegetation cover recorded in a plot, and calculated using the formula;

$$\text{Proportion} = (\%\ \text{cover single species} / \text{total}\ \%\ \text{cover all species}) * 100 \quad [3]$$

The plant species with the highest proportional abundance within a plot equated to the most dominant species. Using these data, the most dominant species was determined for each plot in each survey, allowing comparisons to be made between the grazed and ungrazed treatments. The magnitude of dominance was also assessed by comparing the proportional abundance of the dominant species to that of other abundant species within the same plot. In this study, species were considered "abundant" if they were present in at least four out of the eight sequential surveys, and if they had a percentage cover of 10% or higher per treatment in at least three out of the six plots. Linear mixed-effects models were used to statistically compare the proportional abundance of species within the same plot, through calculation of the mean difference and *t* values. These models used arcsine-transformed "proportional abundance" as the dependent variable, and "species" as the fixed factor, with "plot" nested within "survey" as random factors. Data from grazed and ungrazed treatments were analysed separately.

Results and Discussion

There was a significant effect of grazing treatment on *C. helmsii* abundance ($t_{(87)} = 28.974$, $P < 0.001$), with mean *C. helmsii* abundance found to be lower in the ungrazed plots than in the grazed plots. The abundance of *C. helmsii* was found to decrease over time in the ungrazed plots, while remaining constant in the grazed plots (Figure 1). Measurements of the maximum *C. helmsii* height suggest a trend for taller growth in the ungrazed plots during June to October 2013 (Figure 2). There was also a significant effect of grazing treatment on co-occurring vegetation abundance ($t_{(87)} = 6.264$, $P < 0.001$), and on co-occurring species diversity ($t_{(87)} = 2.647$, $P = 0.010$). Mean abundance was consistently higher in the ungrazed plots, and mean species diversity was higher in the ungrazed plots in all but the first two surveys of the experiment (Figure 3). The mean maximum height of vegetation was found to be consistently higher in the ungrazed plots (Figure 4).

These results indicate that *C. helmsii* benefitted from the presence of grazing disturbance. Indeed, the decline in *C. helmsii* abundance recorded in the ungrazed plots suggests that the very high abundance of *C. helmsii* along the lake drawdown zone of the study site might in part have been maintained as a result of the grazing regime. It is

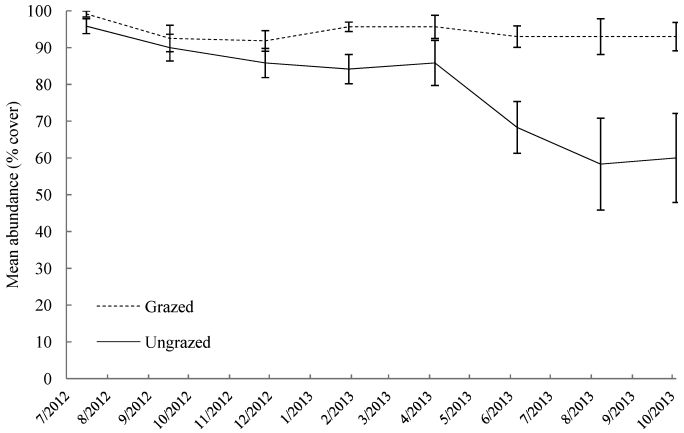


Figure 1. The mean percentage cover (± 1 SE) of *Crassula helmsii* in grazed and ungrazed plot treatments.

hypothesised here that *C. helmsii* benefitted from grazing because this disturbance removed or suppressed other competitive plant species. This hypothesis is supported by the results from the ungrazed plots, where co-occurring vegetation was more abundant, taller, and more diverse. Furthermore *C. helmsii* produced taller vertical growth in the ungrazed plots, which is interpreted here as being indicative of a response to greater light limitation. This explanation is consistent with Olff and Ritchie (1998) who discuss how, in sites where nutrients and water are nonlimiting (as was the case at Kingfishers Bridge; Beecroft et al. 2007; unpublished data), tall plants that compete strongly for light are likely to dominate the plant community in the absence of grazing.

As well as benefitting from the removal of competitors, the traits of *C. helmsii* could have made this species especially well-adapted to the conditions in the grazed plots. First, *C. helmsii* has a high propensity to grow and establish from stem fragments (Dawson and Warman 1987; Hussner 2009), and thus trampling, which caused fragmentation, is unlikely to have greatly hindered *C. helmsii* growth and abundance. Second, *C. helmsii* can grow

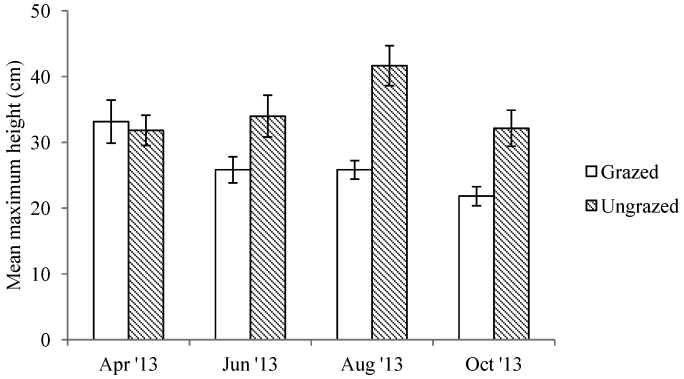


Figure 2. The mean maximum height (± 1 SE) of *Crassula helmsii* in grazed and ungrazed plot treatments.

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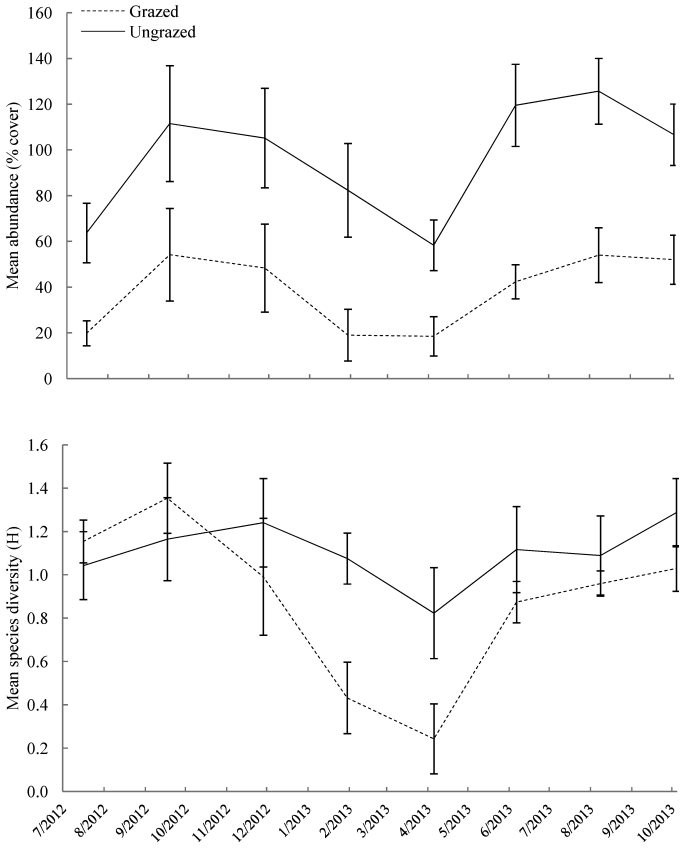


Figure 3. The mean percentage cover and species diversity (Shannon-Weiner H) (± 1 SE) for co-occurring vegetation (all plant species excluding *Crassula helmsii*) in grazed and ungrazed plot treatments.

from nodes along creeping stolons (Dawson and Warman 1987; EPPO 2007) and so it might have been able to compensate for any shoot tip damage it incurred. A light grazing regime might in fact represent highly suitable conditions for *C. helmsii* to thrive, relative to its competitors.

The semicontrolled design of this experiment, wherein access to specific plots was controlled, and the fact that the

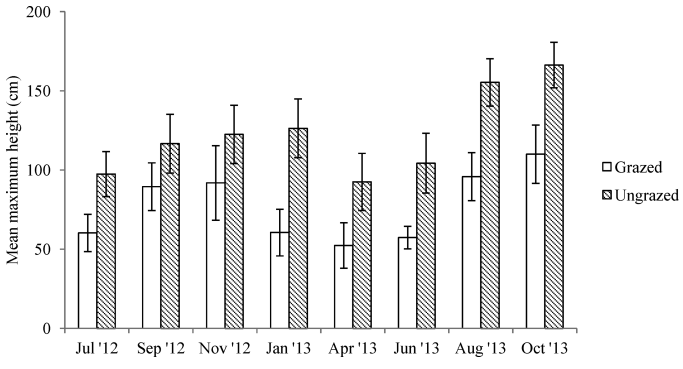


Figure 4. The mean maximum height (± 1 SE) of all vegetation in grazed and ungrazed plot treatments.

treatment plots were monitored over a period of 15 mo, meant that it could be reasonably assumed that the effect on *C. helmsii* abundance observed was due to the experimental treatment and not due to another covariate. It is acknowledged that it would be beneficial to repeat this experimental design at additional study areas in order to ascertain whether similar results are obtained under varying habitat conditions and grazing regimes. This additional replication would increase knowledge of how widely applicable was the observed relationship between *C. helmsii* abundance and grazing disturbance.

In future replications of this study, the experimental design could be improved by including additional data collection and investigation of the feeding behavior of the vertebrate grazers. Observation of what animals fed on the drawdown zone, especially during the initial months after the setup of the plots, would indicate which animals (e.g., wildfowl, sheep, buffalo) were removing the competitors of *C. helmsii*. In the present study, it was not known how extensively *C. helmsii* was grazed; although sheep and waterfowl have previously been seen to graze on the *C. helmsii* at this site (C. J. Cadbury, personal communication), during our experiment the *C. helmsii* vegetation did not appear to be "cropped"; instead, it formed a dense vegetative mat of between 200 and 400 mm (in height. Observation of the vertebrate grazers on the drawdown zone could also be used to determine whether animals graze *C. helmsii* and if so, how frequently.

In both grazed and ungrazed plots there was a clear subset of plant species that dominated the community. Based on the criteria for abundance detailed in the methods section above, two species were classed as abundant, and therefore dominating, in the grazed plot treatments: *C. helmsii* and water mint (*Mentha aquatica* L.). In the ungrazed plots three species were classed as abundant: *C. helmsii*, great willowherb (*Epilobium hirsutum* L.), and *M. aquatica*. There were a number of other species that occurred in four or more surveys; however, the percentage cover of these species was not high enough to meet the criteria (Figure 5). *C. helmsii* remained the most dominant species throughout the experiment in both grazed and ungrazed plots, with the next most abundant species having significantly lower proportional abundance. However, the dominance of *C. helmsii* was less distinct in the ungrazed plots, with lower mean difference and *t* values (Table 1; Figure 6).

Again, these results indicate that the very high community dominance of *C. helmsii* in the study area might have been aided by the presence of large vertebrate grazers, and that in the absence of such disturbance, tall competitive species such as *E. hirsutum* can dominate to a similar extent. Nevertheless *C. helmsii* was not excluded by the increased abundance of these competitors; it persisted as a ground layer underneath the canopy of taller vegetation throughout the experiment. A longer-term

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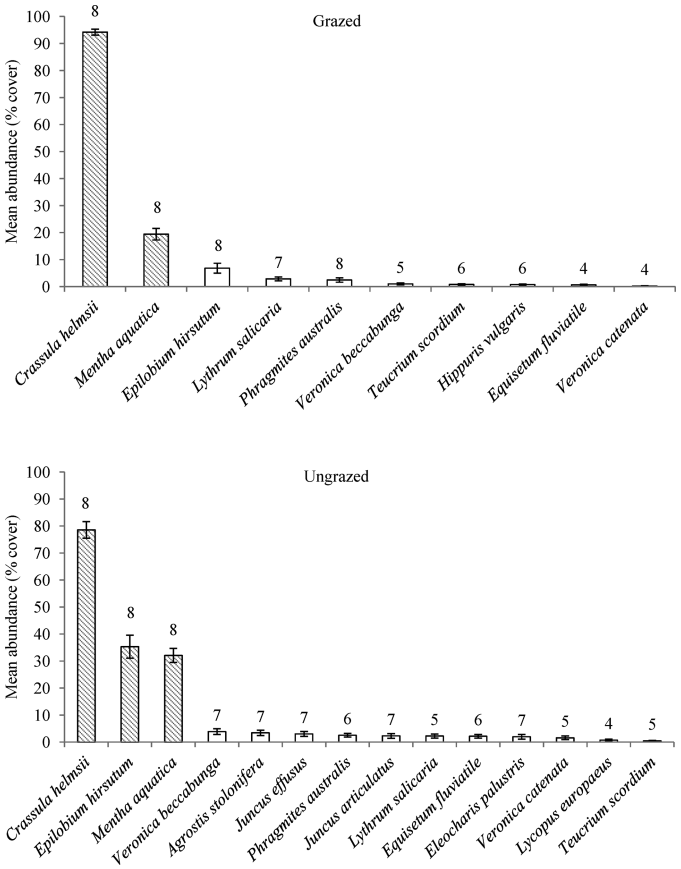


Figure 5. Abundant and frequently occurring plant species recorded in grazed and ungrazed plot treatments. Species classed as ''abundant'' (shaded bars) had a cover of 10% or higher in at least three of the six plots, and in at least four of eight the sequential surveys. Species that were classed as ''frequent'' (no fill) were recorded in at least four of eight the sequential surveys. Species are presented in rank order of mean abundance (± 1 SE), and data labels refer to the number of surveys in which each species was recorded.

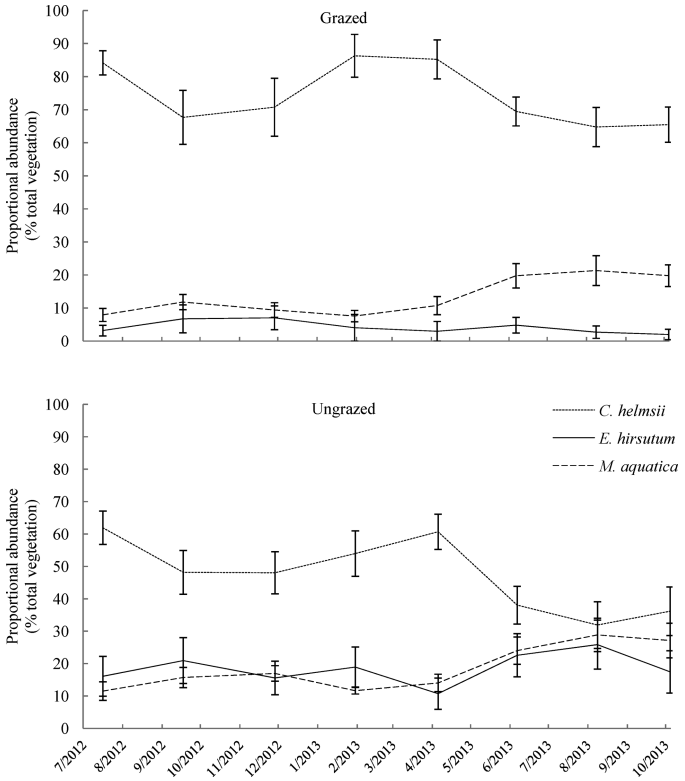


Figure 6. The mean proportional abundance (± 1 SE) of *Crassula helmsii*, *Epilobium hirsutum*, and *Mentha aquatica*, in grazed and ungrazed plot treatments.

study, continued over a number of years, could determine if *C. helmsii* would continue to decline under conditions of increased light competition, or whether it would persist at a lower abundance. In general, the co-occurring plant species (i.e., not *C. helmsii*) had higher mean abundances in the ungrazed plots compared to the grazed plots (Figure 5). A notable exception to this pattern was shown by *Teucrium scordium*, which had a higher mean abundance and frequency in the grazed plots (Figure 5). Indeed, it is known that *T. scordium* prefers open habitat such as drawdown zones, and the unmanaged growth of taller, shading vegetation has been linked to the decline of *T. scordium* (Beecroft et al. 2007).

The aim of this study was to test whether the presence of grazing disturbance affected the relative abundance of *C. helmsii*, and to ascertain whether this was a suppressive or facilitative effect. The results presented here indicate that the presence of large grazing vertebrates facilitates *C. helmsii* abundance and community dominance. As such, the invasion of *C. helmsii* is particularly problematic for land managers who want to use light livestock grazing

Table 1. The results of linear mixed-effects models, comparing the proportional abundance of the most dominant species *Crassula helmsii* to the proportional abundance of the next most abundant species, *Mentha aquatica* and *Epilobium hirsutum*. Data from grazed and ungrazed plot treatments were analyzed separately.

Comparison	Treatment	Mean difference	SE	*t*	df	P
C. helmsii and *M. aquatica*	Grazed	−34.054	2.150	−15.838	47	< 0.001
C. helmsii and *M. aquatica*	Ungrazed	−13.424	1.554	−8.637	47	< 0.001
C. helmsii and *E. hirsutum*	Ungrazed	−16.687	2.115	−7.889	47	< 0.001

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animals in fen habitat as a way of creating patches with a short and open vegetation structure. Rather than increasing species diversity or encouraging particular species that are specialists of this microhabitat, as is the purpose of this management strategy, the use of light grazing might instead serve to encourage *C. helmsii*.

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