New Journal of Botany

# The growth of the non-native Crassula helmsii increases the rarity scores of macrophyte assemblages in south-east England.

--Manuscript Draft--

| | |
|---|---|
| Manuscript Number: | NJB104R1 |
| Full Title: | The growth of the non-native Crassula helmsii increases the rarity scores of macrophyte assemblages in south-east England. |
| Article Type: | Original Research Paper |
| Corresponding Author: | Tim Smith<br>Canterbury Christ Church University<br>UNITED KINGDOM |
| Corresponding Author Secondary Information: | |
| Corresponding Author's Institution: | Canterbury Christ Church University |
| Corresponding Author's Secondary Institution: | |
| First Author: | Tim Smith |
| First Author Secondary Information: | |
| Order of Authors: | Tim Smith |
| | Phil Buckley |
| Order of Authors Secondary Information: | |
| Funding Information: | |

Cover sheet [author names and contact details: information NOT passed to reviewers]

**<u>The growth of the non-native *Crassula helmsii* increases the rarity scores of macrophyte assemblages in south-east England.</u>**

Tim Smith (corresponding author) and Phil Buckley

tim.smith@canterbury.ac.uk

Canterbury Christ Church University,

North Holmes Road,

Canterbury,

Kent.

CT1 1QU.

phil.buckley@canterbury.ac.uk

# The growth of the non-native *Crassula helmsii* increases the rarity scores of macrophyte assemblages in south-east England.

## Abstract

The impact of invasive species on native species is often overlooked. Anecdotal and unmeasured evidence often gains more notice as more empirical research is not available. This study examined the impact of the aquatic invasive species *Crassula helmsii* across a range of waterbody and landscape types in south east England. Plant species lists were compiled for both invaded and uninvaded sites. Scoring systems using both national and county level indices were used to give a measurement of species rarity.  The results showed how invasion has not caused species diversity reductions. Examination of the results has shown how species assemblages have been altered, but often favouring rarer species. Explanations for these findings are discussed. Limitations of the findings including translation to other species and to other geographical areas are also discussed.

## Keywords

Invasive, Non-native, Diversity loss, Conservation, Aquatic macrophyte.

## Introduction

The processes that underlie invasion impacts on plant communities are complex and often poorly understood (Emery and Gross, 2007, Gooden and French, 2015). Plant invasions can lead to a loss in native plant diversity (Leach, 1999, Fierke and Kauffmann, 2006, Michelan et al., 2010, Andreu et al., 2011). These losses could be caused by mechanisms such as direct competition (Gerber et al.,2008), propagule pressure and vector delivery systems (Fierke and Kauffmann, 2006) and poor management decisions (Burke and Grime, 1996, Kimball and Schiffman, 2003, Dostal et al., 2013).

The idea of species loss due to invasion has been challenged. Invasive species may not always be detrimental towards native species (Denoth and Myers, 2007). Poor experimental design may account for some of the examples of species loss by invasions (Wardle, 2001). Changes over time may also show very different results, with initial detrimental impacts changing after prolonged presence of an invasive (Dostal, 2013). In their study of invasive plant species, Bernard-Verdier and Hulme (2014) found that only 10% of the alien species that they studied caused statistically significant declines in species richness.

Species assemblage changes after invasion may also be scale dependent. On a small scale, changes may indicate species loss, whilst at landscape level species losses may not be observable (Michelan et al., 2010). Powell et al. (2013) showed how differences exist when examining invasive mediated reductions in diversity on a smaller scale of less than 25m$^2$. When this was compared to areas at landscape level, no evidence of a reduction in species diversity was found.  The effects of non-natives have been shown to be specific to the individual non-native itself (Hejda et al., 2009).

Species extinctions are often cited as a possible consequence of invasion, but little evidence exists to support this idea. In a comparison of IUCN Red List Species, only 6% of listed species were shown to be at possible risk from invasive species, whilst 33% were shown to be at risk due to habitat loss (Guevitch and Padilla, 2004). These two risks to species loss often occur in conjunction, which makes extracting the true threat caused by invasive species difficult to evaluate.

It was traditionally thought that high species diversity makes a habitat more resilient to invasion (Elton, 1958). Such resilience has been shown to occur in terrestrial systems, where invasive grass species have been shown to be limited by more diverse native macrophytes assemblage (Michelan, 2010). This theory, known as invasion resistance, has been challenged by studies that have shown that native species and invasive species can increase positively together (Stohlgren et al., 1998, Harris et al., 2004). A comparison between island sites that supported three times the number of invasive species compared to mainland sites was carried out (Lonsdale, 1999). Island sites were found to have a comparable level of native diversity to the mainland (Lonsdale, 1999). Highly diverse systems have been shown to be stochastic, energetic systems with the likelihood of species rotations being likely as one species is lost and another replaces it (May, 1973, Huston and DeAngelis, 1994). This rotation may allow invasive species to enter a system, and so be positively correlated with greater diversity.

Invasive species may not be detrimental to rarer native species. *Lythrum salicaria* (Purple loosestrife), invasive in Canada, was shown not to reduce the growth of *Sidalcea hendersonii* (Henderson's mallow) over a 20 year study period (Denoth and Myers, 2007). *Ulex europeaus* (gorse), a common and native species in the UK but an invasive species in New Zealand, has been shown to promote the growth of some groups of species in New Zealand. This resulted in increased species richness when compared to uninvaded control survey sites (Harris et al., 2004).

Lentic freshwater waterbodies have attracted little attention in ecological research, with little regular data collection or monitoring (Williams et al., 2003), with streams, rivers and lakes being a more popular waterbody to study. Aquatic macrophyte diversity is generally lower in ponds and ditches than rivers and streams. Ponds and ditches can however still contain rarities that the rivers and streams do not (Williams et al., 2003). Lentic systems are also an important factor in habitat wide diversity measures, acting as stepping stones between the larger catchments. Though these species pathways may initially seem beneficial to landscape scale diversity, increasing species movement of native macrophytes is also likely to encourage invasive dispersal. Macrophyte species richness has however been found to correlate positively to the number of neighbouring waterbodies within a 500m radius (Oertil et al., 2002).

Small, temporary ponds and ditches are capable of acting as biodiversity rich areas, capable of supporting species that are unable to thrive in the larger, permanent systems (Cereghino et al., 2008). Temporary ponds were shown to make up 40% of lowland ponds within Britain in the Lowland Pond Survey (Nicolet et al., 2004).On a scaled measure of the larger, more well studied systems, temporary ponds are often more diverse than their permanent comparatives (Cereghino et al., 2008). It has also been shown that a collection of smaller ponds has a greater rarity value (ie. more rarities present) than a similar combined sized single pond (Oertil et al., 2002).

*Crassula helmsii* is an aquatic plant capable of growing in a number of forms and occupying a range of niches in riparian and freshwater habitats. It was first recorded in a natural system in 1956 in Essex (Dawson and Warman, 1987). Due to its rapid spread since then, and its ease of reproduction through asexual methods, it has been categorised as an invasive species. *C. helmsii* was predicted to be spread quickly across the country, with initial research showing it to be capable of excluding all other species, thus creating a low diversity monoculture (Leach, 1999). After this date however, minimal published evidence exists to support this, with the only other published study showing no significant impact towards native plant species (Langdon, 2004). No large scale investigations to date have investigated the plant in a range of habitats, to show in-field responses to plant diversity after invasion by *C. helmsii*.

The aim of the macrophyte study was to investigate whether invasion by *C. helmsii* had a negative effect on macrophyte diversity on a range of sites in the south east of England.

## Materials and Methods

18 sites were visited in Kent and East Sussex, comprised predominantly of nature reserves and country parks. Where possible, both invaded and uninvaded lentic habitats were surveyed at each site, in an attempt to reduce environmental and geographical variation. This resulted in a total of 78 individual sampling locations, with 57 supporting *C. helmsii* and 21 uninvaded control sites. A greater number of *C.helmsii* sites were surveyed due to the level of colonisation at some sites resulting in a reduced number of available sampling locations being available.

Plants were identified and recorded along a 10m section of the riparian margin of the waterbody. The riparian margin studied was inclusive of the winter high water line, which was visible during the summer surveying season due to either a sudden species composition change or a band of dead plant material. Aquatic plants within 5m of the waterline were also recorded, with species present limited due to identification by visual methods only. Unknown specimens that could not be visually identified or keyed out in the field were photographed for later analysis.

Plant species lists for each site visited were scored in accordance to 3 scoring systems for rarity. These were:-

- The Botanical Society for the British Isles (BSBI, 2013)
- The Predictive System for Multimetrics (PSYM – Howard, 2002)
- A New Atlas of Kent Flora (Philp, 2010)

The national systems (BSBI and PSYM) measure rarity by the number of 10km x 10km hectads where the species is present. The county level scoring system (Philp, 2010) measure rarity in the same way, but by using 2km x 2km tetrads, due to the increased level of surveying detail. The idea of rarity therefore allows a measure of species composition to be ascertained. The BSBI scores were ranked from 16 (rarest) to 1 (most common), with a 250 hectad separation between each scoring integer.

The PSYM (Predictive System for Multimetrics) is a scoring system that assesses the biological quality of lentic waters in England and Wales (Howard, 2002). It provides scores only for aquatic macrophytes, and does represent riparian species. The PSYM scoring metric was included within the analysis to ascertain how it related to the other scoring systems that provided scores for all plant species.

The localised scoring system by Philp (2010) is based on plant scores derived just from Kent, and so are used to give a county level score. This was included to give a more localised scoring representation than the national databases. The Kent scoring metric was ranked from 21 (rarest) to 1(most common), with a 50 tetrad separation between each scoring integer (based on a total tetrad score for the county of 1043).

Total rarity scores were calculated for each survey location, with subsequent analysis of average values for each survey location generated by dividing the total rarity score by the total number of species.

$$Average\ rarity\ score = \frac{Total\ rarity\ score}{Total\ species\ number}$$

**Equation 1. Calculation of the average rarity score for each survey location, using the database rarity scores and measured species numbers from each location surveyed.**

To ascertain whether *C. helmsii* was having an effect on native flora, sites were divided into invaded and clear (control) sites. This enabled a comparison of the previously constructed scores to be carried out. Data analysis was by Mann Whitney analysis, with sample numbers of n=57 for *C. helmsii* sites, and n=21 for control sites.

Each of the survey locations were categorised by its dominant landscape habitat. This provided three distinct habitat types of coastal, lake and woodland. Previously calculated rarity scores were subdivided into each of these categories, and analysed in a similar manner using Mann Whitney between control and invaded sites.

Waterbody types were analysed in a similar manner, with the categories of ditches, lakes and ponds being used. As for habitat comparisons, only the average rarity scores for each location were used in the comparison, using Kruskal Wallis tests.

## Results

There were significant differences between control and invaded sites for 2 of the 3 rarity scores - BSBI ($p$ = 0.0126) and Kent 2010 ($p$ = 0.0016) (table 1). The box plots (Fig. 1) show that the higher rarity values are shown by the sites where *C. helmsii* is present.

Analysis of the 3 habitat subdivisions of coastal, lake and woodland showed significant differences between invaded and control site (table 1). Coastal habitats comparisons returned significantly different results for total rarity scores for BSBI ($p$ = 0.0072) and Kent 2010 ($p$ = 0.0457) scoring systems, and total species number for PSYM ($p$ = 0.0443). The box plots (Fig. 2) show that higher total rarity scores were found on *C. helmsii* sites for the two scoring systems. The PSYM total species number was found to be significantly higher on the *C. helmsii* survey locations. No significant results were returned for lakeside comparison. For woodland comparison, the Kent 2010 ($p$=0.0092) average rarity score was found to be significantly different, with box plots (Fig. 3) showing that the higher scores were found on *C. helmsii* survey locations.

Comparison of water body type by Kruskal Wallis analysis found that all rarity scoring systems were significantly different when analysed - BSBI ($p$=0.001), PSYM ($p$=0.002), Kent 2010 ($p$=0.024). For each scoring system, ditch systems showed the highest average rarity score.

## Discussion

The results demonstrated some evidence of increased average rarity scores on invaded sites. Scoring systems that included both the riparian and aquatic species compositions (BSBI and Kent 2010) showed increased average rarity scores with the presence of *C. helmsii.* The PSYM methodology did not show any significant difference between these invaded and control sites. This may be due to only aquatic and not riparian species being included in the PSYM scoring system. As *C. helmsii* is able to grow across a range of habitat morphologies, not including the full range of riparian species does not provide an accurate representation of the in-field situation. These results indicate that sites supporting *C. helmsii* have a significantly increased rarity score, and therefore 'rarer' species growing on them, in comparison to the *C. helmsii* absent control sites. When considering the PSYM scoring system, no detrimental effect could be found just for the aquatic species included in the analysis, but neither did it show any promotion of rarer species growth.

The majority of coastal sites surveyed were ditch systems with a diverse terrestrial species composition upon the bankside habitat. The significantly different total rarity scores for the other two scoring systems may be due to species numbers being lower on invaded coastal sites compared to coastal control sites. An average of 12 species were found on invaded sites, compared to 8.8 on control sites. This was the only habitat type to show an average decrease of species on invaded compared to control sites (Lake sites were 12.1 on invaded, 15.4 control, woodland sites were 9.8 on both invaded and control). Any changes to species composition would therefore have had an amplified effect on total rarity scores on invaded sites compared with control sites. The average diversity scores were not found to be significantly different between invaded and control coastal sites. It therefore may be that these results are a reflection of low initial diversity, which was susceptible to statistical change due to *C. helmsii* being included in the analysis. It may also be due to the ability for *C. helmsii* to alter the chemical component of the water bodies after invasion. It is known to have the ability to accumulate heavy metals (Küpper et al., 2009). If this accumulation extends to other components of saline water, it may allow plant species to grow here that would not have been able to pre-invasion. As only a small range of chemicals were studied, it is difficult to reach conclusions on this. Further investigations of a larger range of metals and nutrients would be required.

Woodland habitat results indicated an increase in the average rarity score for the county level scoring system.  As this is limited to just Kent, and was not found for the other scoring systems, it may be a regional effect, and so would require further studies outside of the county to support it. The reduction in light levels at the woodland sites may have limited growth of *C. helmsii* due to a limitation of photosynthetic activity.  Though it is able to grow under low light levels (Hussner, 2009), its ability to use the CAM system of photosynthesis is better utilised under high light levels (Newman and Raven, 1995, Klavsen and Maberly, 2010). The fact that control ponds had a lower average rarity score may be descriptive of a dominance of native flora preventing invasion and subsequent opportunistic native species, which would lead to increases in the average rarity score of the site. This is different to previous studies of *C. helmsii,* where species losses were thought to occur (Leach, 1999). This example was, however, a small scale study limited to selected ponds. A wider ranging study found no loss in macrophyte species numbers (Langdon, 2004), but gave no description of the macrophyte composition of the sites being studied.

The Kruskal Wallis analysis of the invaded habitats showed that significant differences existed between all waterbody types.  This demonstrates that the creation of a monoculture after invasion by *C. helmsii* did not occur, and that the natural variation in species composition remained.

A study of waterbody types for macrophyte diversity found that natural variations do occur in species diversity, even when removing plant invasions as a variable (Williams et al., 2003). In Williams' study, rivers (not included in the *C. helmsii* study due to its inability to grow in flowing water in natural systems) were the most diverse, with ditches being the least diverse but able to support rarities. In the *C. helmsii* study, ditch systems consistently scored the highest for rarity. Species numbers between sites were not found to differ significantly, and so this is only partially supported by the evidence. As rarity scores for sites have not been previously measured, it is difficult to judge whether invasion by *C. helmsii* has had an effect on these systems, or whether it merely reflects the presence of greater numbers of rarer species in ditches. If it is considered with the previous comparison of invaded against control sites, it may be that it is showing evidence of invasion facilitating an increase in rarer species. Ditches, with naturally lower diversity, may be able to accommodate a greater number of these species along with *C. helmsii*. This theory of increased exotics and increased natives co-occurring has been shown by previous studies (Stohlgren et al., 1998, Smith et al., 2006).

Ponds are known to be highly diverse systems, with a number of studies showing their significance within the waterbody network (Linton and Goulder, 2000, Biggs et al., 2005, Cereghino et al., 2008). However, due to their ability to act as nutrient sinks for the wider landscape, they are often at risk of disturbance from resource fluctuations and sudden changes (Cereghino et al., 2008). The *C. helmsii* study has shown that pond systems have consistently had the lowest rarity scores when compared to ditches and lakes. Previous research on ponds has shown them to be the most diverse of lentic systems (Williams et al., 2003). This may indicate a larger impact on ponds than other lentic systems after invasion by *C. helmsii*, if the high diversity scores are assumed for this study. One possible explanation may be that the greater original diversity is unable to prevent invasion, but is able to prevent colonisation by opportunistic natives that may be able to exploit the new niches opened during invasion by *C. helmsii*.

This study has shown that species numbers have not significantly decreased due to invasion by *C. helmsii*, but the average rarity score of the species present on invaded sites has increased. This would seem to indicate a change in species composition, towards rarer species on the invaded sites. Rodriguez (2006) suggests mechanisms as to how this may have occurred, of which habitat modification and competitive release may be applicable to *C. helmsii*. Habitat modification may be achieved by the addition of both structures for adherence of new species, or sheltered areas that allow for growth of macrophytes that may not have been present without C. helmsii biomass being present. This has been shown to occur for *Spartina alterniflora* (Smooth Cordgrass), which stabilises cobble beach habitats, thereby reducing disturbance and facilitating the growth of *Suaeda linearis* (Annual Seepweed) and *Salicornia europaea* (Common Glasswort) (Bruno and Kennedy, 2000). This may occur with *C. helmsii*, whereby sheltered areas create catchments for floating species such as the *Lemna* spp. (duckweeds), and *Hydrocharis morsus-ranae* (frogbit), which may otherwise have been dislodged due to wind disturbance.  *Lemna minor*, *Lemna trisulca* and *H.morsus-ranae* were recorded at some survey locations in this study, and so may explain the possible increases in rarity scores with *C. helmsii* present.

Competitive release of rarer species due the reduction of a dominant native species may have occurred (Rodriguez, 2006), which could also facilitate the growth of *C. helmsii* (Emery and Gross, 2007). The ability for non-native species to alter species compositions in favour of rarer species and thereby create more diverse habitats has been exploited in ecological restoration (D'Antonio and Meyerson, 2002, Zarnetske et al., 2013). This release from competition by dominant native plant growth may be due to trophic interactions (Wonham et al., 2005).A study of riparian macrophytes found that natives and non-natives were able to exploit nitrogen deposits on an equal basis (Bradford et al., 2007), and not competitively exclude each other.

The response by non-natives to environmental changes has been shown to vary between different species, with some being a passenger to change rather than the genesis of change itself (Didham et al., 2005, MacDougall and Turkington, 2005, Bernard-Verdier and Hulme, 2014). These environmental stresses have been shown to have varying effects on both natives and non-natives (Turkington and Bradfield, 2006), and are dependent on the species and habitats being studied (Woitke et al., 2002, Didham et al., 2007). Whether an environmental stress has occurred as a precursor to loss of native dominance or whether invasion by *C. helmsii* was responsible for the decline in dominance is not clear from this study. MacDougall and Turkington (2005) suggest an appropriate method of testing this 'passenger' theory, with the removal of the invasive resulting in the increase in diversity of other, novel native species. This is likely to be a difficult procedure to replicate for *C. helmsii*, due to the difficulty in removing the species (Dawson and Warman, 1987), but may help to provide evidence for the reason why it has colonised successfully.

This interaction between non-native species and rarer species has been shown to have a mutualistic response in other studies (Harris et al., 2004, Denoth and Myers, 2007). A study of riparian and upland habitats in the USA showed increases in exotic species and native species occurring simultaneously (Stohlgren et al., 1998). Though the *C. helmsii* results do not show increases in species numbers, it does illustrate how species loss may not always follow invasion.

Though the BSBI and PSYM scoring systems are national, the Kent Atlas is a county based score, and so cannot be translated outside of the county to different sites. The effects of *C. helmsii* in other counties may therefore differ, especially as distribution records show *C. helmsii* to be more strongly associated to the south east of England (BSBI Maps, 2015). Invasives have different effects across different countries. A study of *Impatiens glandulifera* (Himalayan Balsam) in the Czech Republic showed that it had little effect upon native community characteristics and species composition , but in the UK *I.glandulifera* has been shown to have detrimental effects towards native species composition (Hulme and Bremner, 2005). The invasive species *Heracleum mantegazzium* (Giant Hogweed) showed an impact upon native plant species, on the same survey sites where *I.glandulifera* was shown not to have an impact towards natives (Pysek and Pysek, 1995, Hejda and Pysek, 2006). These differences were thought to relate to the morphology of the plant species, and the ability to compete for light more successfully (Hejda et al., 2009).

Further factors could be considered when examining the results and statistical output. The idea of habitat scale of the investigation may be important. Experiments have shown that small scale changes are not always represented on a landscape wide basis. A study of three invasive plants; *Dianella ensifolia* (Cerulean flax lily), *Lonicera maackii* (Amur Honeysuckle) and *Morella faya* (Fire Tree) were all shown to cause local decreases in macrophyte diversity (Powell et.al, 2013). When examined on a landscape scale, and compared to control sites, no significant difference of species loss between invaded and control sites could be found.

The length of time that an invasive species is present on a site is also likely to be an important factor. It has been shown that the effect of an invasive macrophyte species decreases over time. Dostal et al.(2013) showed that the effects of *Heracleum mantegazzianum* (Giant Hogweed) decreased between a 48 year separation in sampling time. A decrease in impact by invasives over time was also shown in a study of *Phalaris arundinacea, Rubus armeniacus and Hedera helix* (Fierke and Kauffman, 2006). Morphological and physiological changes of native species may account for this decrease in the effect of invasive species, but require a prolonged selective pressure of invasion to facilitate change (Strayer et al., 2006). The time separation of the Kent scoring systems is only 28years, and so may not show this change. It may be that the scoring system method will indicate how habitats change due to invasion over time. This will require new updated scoring systems in subsequent decades to be developed, which may show how invasions are dynamic processes and liable to changes over time.

The discrepancy between the scoring systems illustrates a flaw in using scoring metric that are not continually updated. The PSYM method and its scoring metrics are, at the time of writing, more than 13 years old (Howard, 2002). The BSBI and Kent 2010 scoring metrics were more recently constructed, with BSBI scores renewed every 2 years (BSBI, 2013).

## **Conclusion**

Though species numbers do not change significantly when comparing invaded and uninvaded sites, species composition does. Average species rarity scores of invaded sites have been shown to increase when compared to control sites. The mechanism for this has been suggested as a reduction in competition from the dominant native species, which not only facilitates invasion by *C. helmsii*, but also promotes other native species to occupy the habitat alongside the non-native. This results in an altered composition of plants, but not a reduction in numbers. The idea of 'rarer' species being present is not necessarily a good thing. If a habitat is being managed to retain a particular composition that is desired, the change towards rarer species may be a negative factor of invasion. There may also be benefits of having rarer species. They may be able to support a wider range of species through the provision of food and shelter that would otherwise have been lacking.

## **Acknowledgements**

This research was part funded by the Botanical Society for the British Isles and Canterbury Christ Church University.

## **References**

Andreu, J., Montserrat, V. 2011. Native plant community response to alien plant invasion and removal. *Managing Biological Invasions*. 2: 81-90.

Bernard Verdier, M., Hulme, P.E. 2015 Alien and native plant species play different roles in plant community structure. *Journal of Ecology*, 103: 143-152.

Biggs, J., Williams, P., Whitfield, M., Nicolet, P., and Weatherby, A. 2005. 15 years of pond assessment in Britain: results and lessons learned from the work of Pond Conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems.* 15: 693-714.

Biological Records Centre. 2013. *Online Atlas of the British and Irish Flora.* Available at: www.brc.ac.uk/plantatlas. (Accessed September and October, 2013).

Botanical Society for The British Isles (2013) *BSBI Maps Scheme: Hectad maps*. Available at: http://www.bsbimaps.org.uk/atlas/main.php. (Accessed September and October, 2013).

Botanical Society for The British Isles (2015) *BSBI Maps Scheme: Hectad maps*. Available at: http://www.bsbimaps.org.uk/atlas/map_page.php?spid=2423.0 (Accessed April, 2015).

Bradford, M.A., Schumacher, H.B., Catovsky, S., Eggers, T., Newingtion, J.E., Tordoff, G.E. 2007 Impacts of invasive plant species on riparian plant assemblages: interactions with elevated atmospheric carbon dioxide and nitrogen deposition. *Oecologia.* 152(4): 791-803.

Bruno, J.F., Kennedy, C.W. (2000). Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora. Oecologia.* 122: 98-108.

Burke, M.J.W., Grime, J.P. 1996. An Experimental Study of Plant Community Invasability. *Ecology*, 77(3): 776-790.

Cereghino, R., Biggs, J., Oertil, B., Declerck, S. 2008. The ecology of European ponds: defining the characteristics of a neglected freshwater habitat. *Hydrobiologia.* 157: 1-6.

D'Antonio, C., Meyerson, L.A., 2002 Exotic plant species as problems and solutions in ecological restoration: A synthesis. *Restoration Ecology*. 10(4): 703-713.

Dawson, F.H., Warman, E.A. 1987 *Crassula helmsii* (T.Kirk) Cockayne: Is it an Aggressive Alien Aquatic Plant in Britain? *Biological Conservation.* 42: 247-272.

Denoth, M., Myers, J.H. 2007. Competition between *Lythrum salicaria* and a rare species: combining evidence from experiments and long-term monitoring. *Plant Ecology*. 191: 153-161.

Didham, R.K.,Tylianakis, J.M., Hutchinson, M.A., Ewers, R.M., Gemmell, N.J. 2005 Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution*. 20(9): 470-474.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M. 2007 Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution.* 22(9): 489-496.

Dostal, P., Mullerova, J., Pysek, P., Pergl, J., Klinerova, T. 2013. The impact of an invasive plant changes over time. *Ecology Letters*. 16: 1277-1284.

Elton, C.S. (1958). *The Ecology of Invasions by Animals and Plants*. London: Methuen.

Emery, S.M., Gross, K.L. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. *Ecology*. 88(4): 954-964.

Fierke, M.K., Kauffman, J.B. 2006. Invasive species influence riparian plant diversity along a successional gradient, Willamette River, Oregon. *Natural Areas Journal*. 26(4): 376-382.

Gerber, E., Krebs, C., Murrell, C., Moretti, M., Rocklin, R., Schaffner, U. 2008. Exotic invasive knotweeds (*Fallopia spp.*) negatively affect native plant and invertebrate assemblages in European riparian habitats. *Biological Conservation*. 14: 646-654.

Gooden, B., French, K. 2015. Impacts of alien plant invasion on native plant communities are mediated by functional identity of resident species, not resource availability. Oikos. 124(3): 298-306.

Guevitch, J., Padilla, D.K. 2004 Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution.* 19(9): 470-474.

Harris, R.J., Toft, R.J., Dugdale, J.S., Williams, P.A., Rees, J.S. 2004. Insect assemblages in a native (kanuka – *Kunzea ericoides*) and an invasive (gorse – *Ulex europaeus*) shrubland. *New Zealand Journal of Ecology.* 28: 35-47.

Hejda, M., Pysek, P. 2006. What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation. *Biological Conservation*. 132: 143-152.

Hejda, M., Pysek, P., Jarosik, V. 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. *Journal of Ecology*, 97: 393-403.

Howard, S. 2002. *Pond Conservation Trust*: *A guide to monitoring the ecological quality of ponds and canals using PSYM*. Available at: http://www.derbyshirebiodiversity.org.uk/news/files/PSYMmanual.pdf. (Accessed January 2013).

Hulme, P.E., Bremner, E.T. 2005. Assessing the impact of *Imaptiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *Journal of Applied Ecology*. 43: 43-50.

Hussner, A. 2009. Growth and photosynthesis of four invasive aquatic plant species in Europe. *Weed Research*. 49: 506-515.

Huston, M.A., DeAngelis, D.L. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist*. 144: 954-977

Kimball, S., Schiffman, P.M. 2003. Differing effects of cattle grazing on native and alien plants. *Conservation Biolgoy.* 17(6): 1681-1693.

Klavsen, S.K., Maberly, S.C. 2010. Effect of light and $CO_2$ on inorganic carbon uptake in the invasive aquatic CAM-plant *Crassula helmsii*. *Functional Plant Biology*. 37: 737-747.

Küpper, H., Kroneck, P.M.H. (2005). Heavy metal uptake by plants and cyanobacteria. *Metal Ions in Biological Systems*. 44: 97–142.

Langdon, S.J., Marrs, R.H., Hoise, C.A., McAllister, H.A., Norris, K.M., Potter, J.A. 2004. *Crassula helmsii* in U.K. Ponds: Effects on Plant Biodiversity and Implications for Newt Conservation. *Weed Technology*. 18: 1349-1352.

Leach, J. 1999. *Crassula helmsii* in the British Isles – an unwelcome invader. *British Wildlife Publishing*. 10(4): 234-239.

Linton, S., Goulder, R. 2000. Botanical conservation value related to origin and management of ponds. *Aquatic Conservation: Marine and Freshwater Ecosystems*. 10: 77-91.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasability. *Ecology*. 80: 1522–1536

MacDougall, A.S., Turkington, R. 2005 Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*. 86: 42-55.

May, R.M. 1973. *Stability and complexity in model ecosystems*. New Jersey, USA: Princeton University Press.

Michelan, T.S., Thomaz, S.M., Mormul, R.P., Carvalho, P. 2010.Effects of an exotic invasive macrophytes (tropical signalgrass) on native plant community composition, species richness and functional diversity. *Freshwater Biology.* 55: 1315-1326.

Newman, J.R., Raven, J.A. 1995. Photosynthetic carbon assimilation by *Crassula helmsii*. *Oecologia.* 101:494-499.

Nicolet, P., Biggs, J., Fox, G., Hodson, M.J., Reynolds, C., Whitfield, M., Williams, P. (2004). The wetland plant and macroinvertebrate assemblages of temporary ponds in England and Wales. *Biological Conservation*. 120: 261-278.

Oertli, B., Joye, D.A., Castella, E., Juge, R., Cambin, D., L, J.B. (2002) Does size matter? The relationship between pond area and biodiversity. *Biological Conservation.* 104: 59-70.

Philp, E. 1982. *The Atlas of Kent Flora.* UK: The Kent Field Club.

Philp, E. 2010. *The New Atlas of Kent Flora.* UK: The Kent Field Club.

Powell, K.I., Chase, J.M., Knight, T.M. 2013. Invasive plants have scale-dependant effects on diversity by altering species-area relationships. *Science*. 339: 316-318.

Pysek, P., Pysek, A. 1995. Invasion by *Heracleum mantegazzium* in different habitats in the Czech Republic. *Journal of Vegetation Science.* 6. 711-718.

Rodriguez, L.F. 2006. Can Invasive Species Facilitate Native Species? Evidence of How, When, and Why These Impacts Occur. *Biological Invasions*. 8(4): 927-939.

Smith, R.M., Thompson, K., Hodgson, J.G., Warren, P.H., Gaston, K.J. 2006. Urban domestic gardens (IX): Composition and richness of the vascular plant flora, and implications for native biodiversity. *Biological Conservation*. 129: 312-322.

Strayer, D.L., Eviner, V.T., Jeschke, J.M., Pace, M.L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*. 21(11): 645-651.

Stohlgren, T.J., Bull, K.A., Otsuki, Y., Villa, C.A., Lee, M. 1998. Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecology*. 138: 113-125.

Turkington, R., Bradfield, G.E. 2006 Patterns of Plant Invasion along an Environmental Stress Gradient. *Journal of Vegetation Science*. 17(1): 47-56.

Wardle, D. (2001). Experimental demonstration that plant diversity reduces invasability: Evidence of a biological mechanism or consequence of sampling effect? *Oikos.* 95: 161-170.

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., Sear, S. 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation.* 115: 329-341.

Woitke, M., Dietz, H. 2002 Shifts in dominance of native and invasive plants in experimental patches of vegetation. *Perspectives in Plant Ecology, Evolution and Systematics*. 5(3): 165-184.

Wonham, M.J., O'Connor, M., Harley, C.D.G. 2005 Positive effects of a dominant invader on introduced and native mudflat species. *Marine Ecology Progress Series.* 289: 109-116.

Zarnetske, P.L., Gouhier, T.C., Hacker, S.D., Seabloom, E.W., Bokil, V.A. 2013 Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *Journal of Ecology*. 101(4): 905-915.

Figure captions

**Figure 1. Boxplots of significant results of direct comparison between *C. helmsii* and control sites.** BSBI average rarity scores (left) and Kent 2010 average rarity scores (right).

**Figure 2. Boxplots of significant results from comparison between coastal habitat types.** Top left = Coastal BSBI total rarity scores. Top right = Coastal Kent 2010 total rarity scores. Bottom left = Coastal PSYM total species number (diversity).

**Figure 3. Boxplots of significant results from comparison between woodland habitat types.** Woodland Kent 2010 average rarity scores.

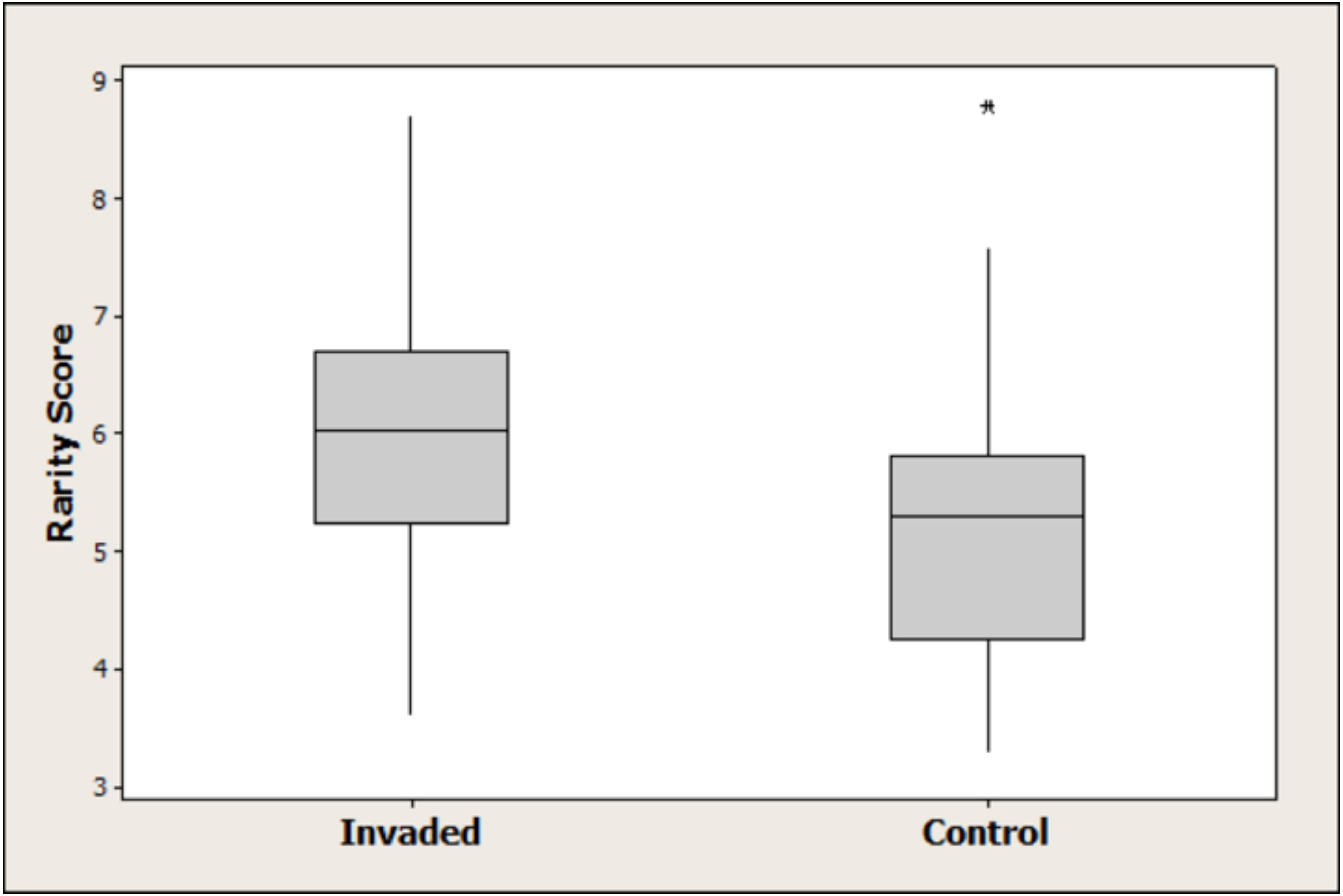
Tables

**Table 1. Probability values from data analysis of plant scoring values, with statistically significantly results highlighted.**

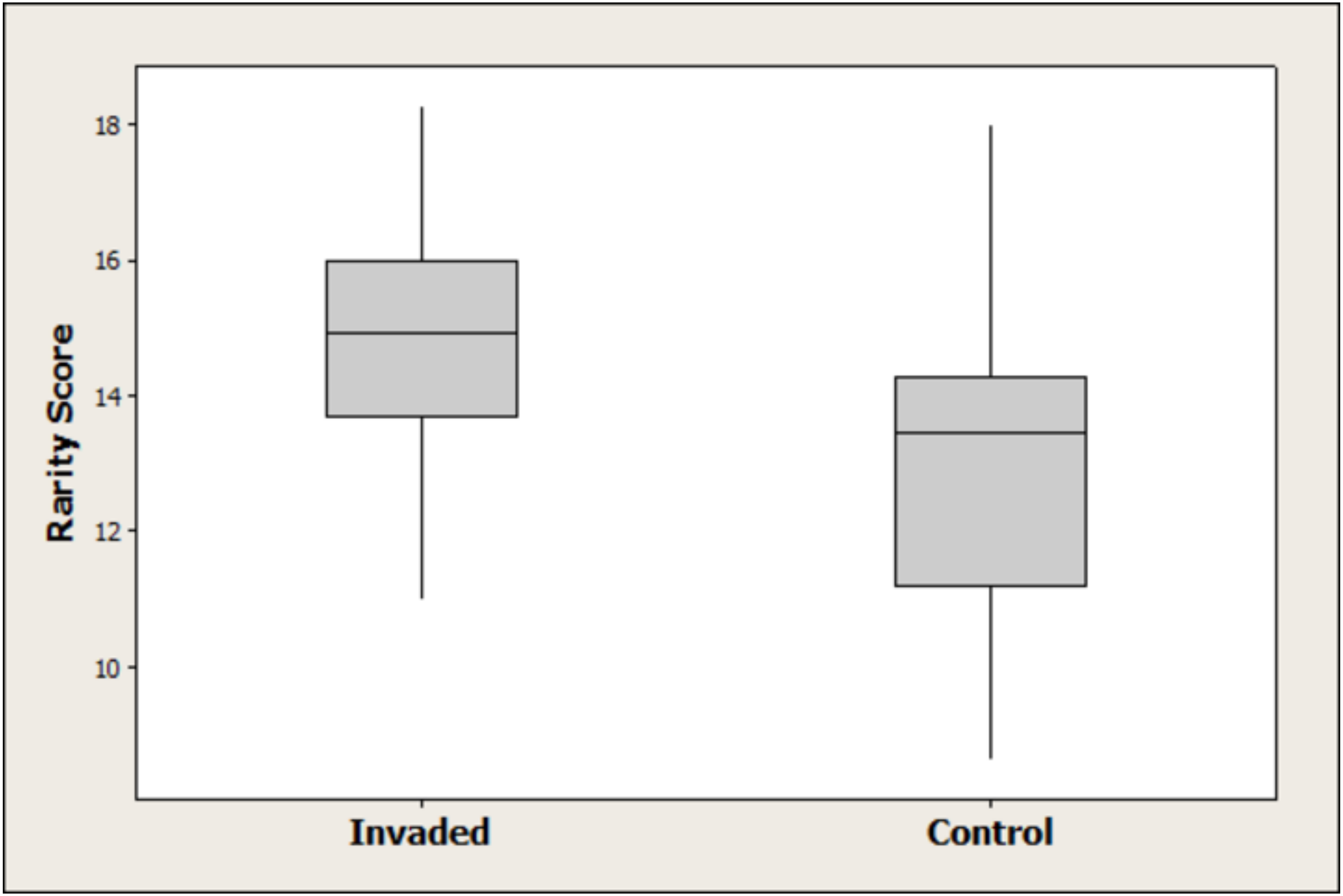
| | *C. helmsii* vs. Control | Habitat | | | Waterbody Type |
|---|---|---|---|---|---|
| | | Coastal | Lake | Wood. | |
| Total Species Number | 0.8565 | 0.0895 | 0.1007 | 0.9548 | 0.2760 |
| BSBI Total Species Number | 0.8432 | 0.0919 | 0.0809 | 0.9545 | / |
| BSBI Total Rarity Score | 0.0932 | 0.0072 | 0.2938 | 0.8648 | / |
| BSBI Average Rarity Score | 0.0126 | 0.6849 | 0.2947 | 0.7767 | 0.001 |
| PSYM Total Species Number | 0.3900 | 0.0443 | 0.1233 | 0.0619 | / |
| PSYM Total Rarity Score | 0.3484 | 0.0351 | 0.0867 | 0.2725 | / |
| PSYM Average Rarity Score | 0.4410 | 0.3467 | 0.8935 | 0.0605 | 0.0020 |
| 2010 Total Species Number | 0.8832 | 0.0899 | 0.1123 | 0.9090 | / |
| 2010 Total Rarity Score | 0.2070 | 0.0457 | 0.1904 | 0.0541 | / |
| 2010 Average Rarity Score | 0.0016 | 0.6619 | 0.1904 | 0.0092 | 0.0240 |

Black&White/ Grayscale figure

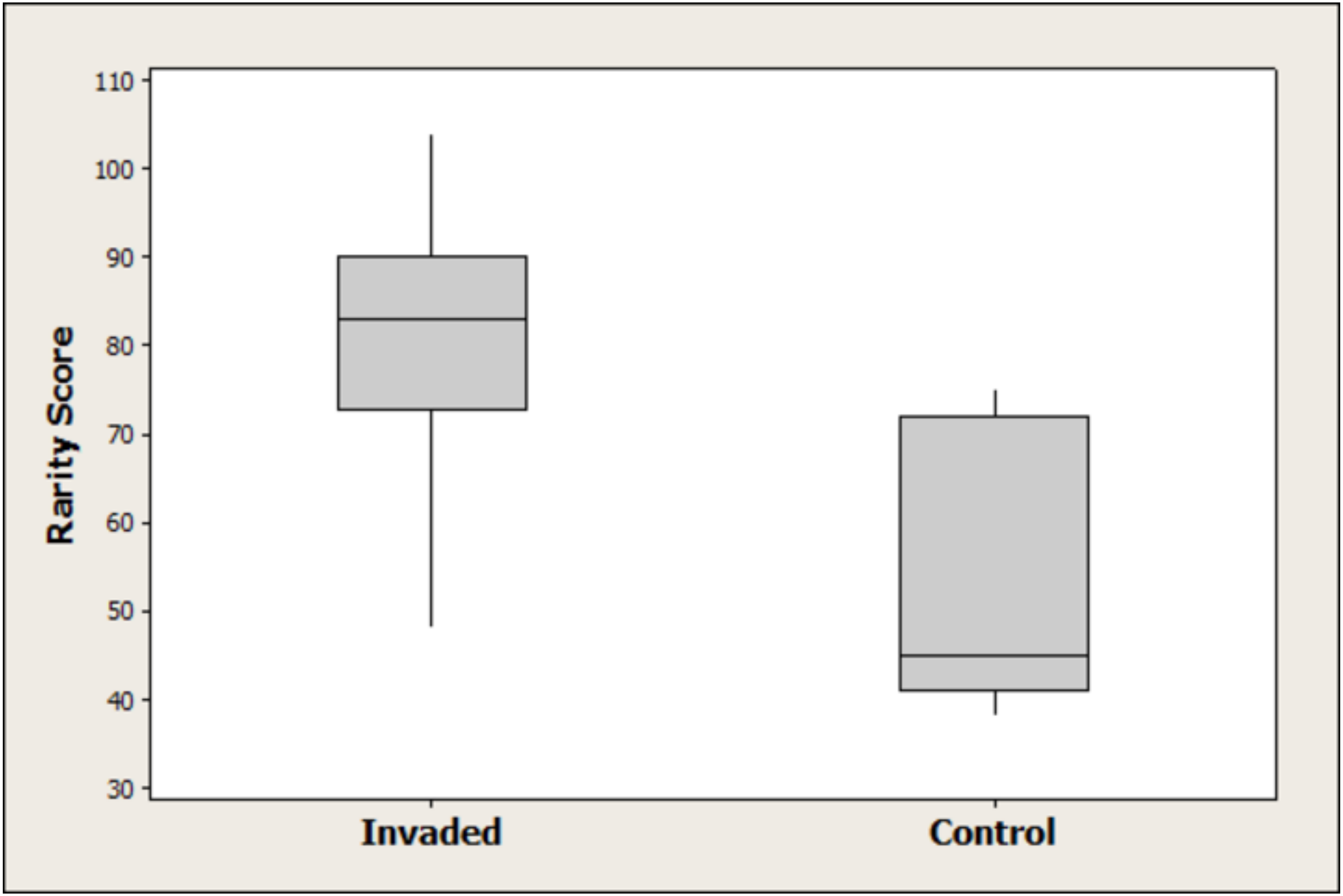
Click here to download Black&White/ Grayscale figure: Fig 1A BSBI average rarity score.tif



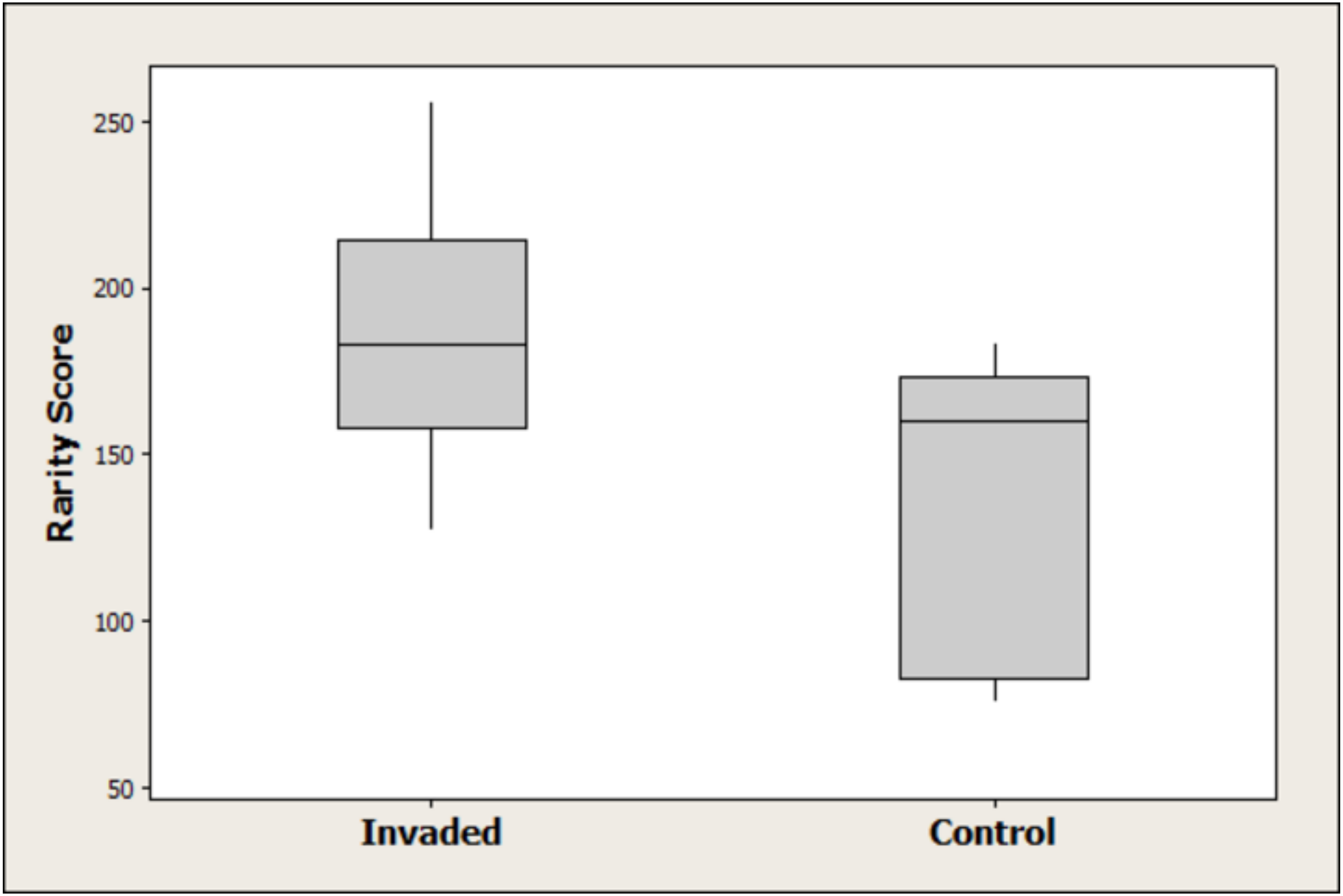
Black&White/ Grayscale figure
Click here to download Black&White/ Grayscale figure: Fig 1B 2010 average rarity score.tif



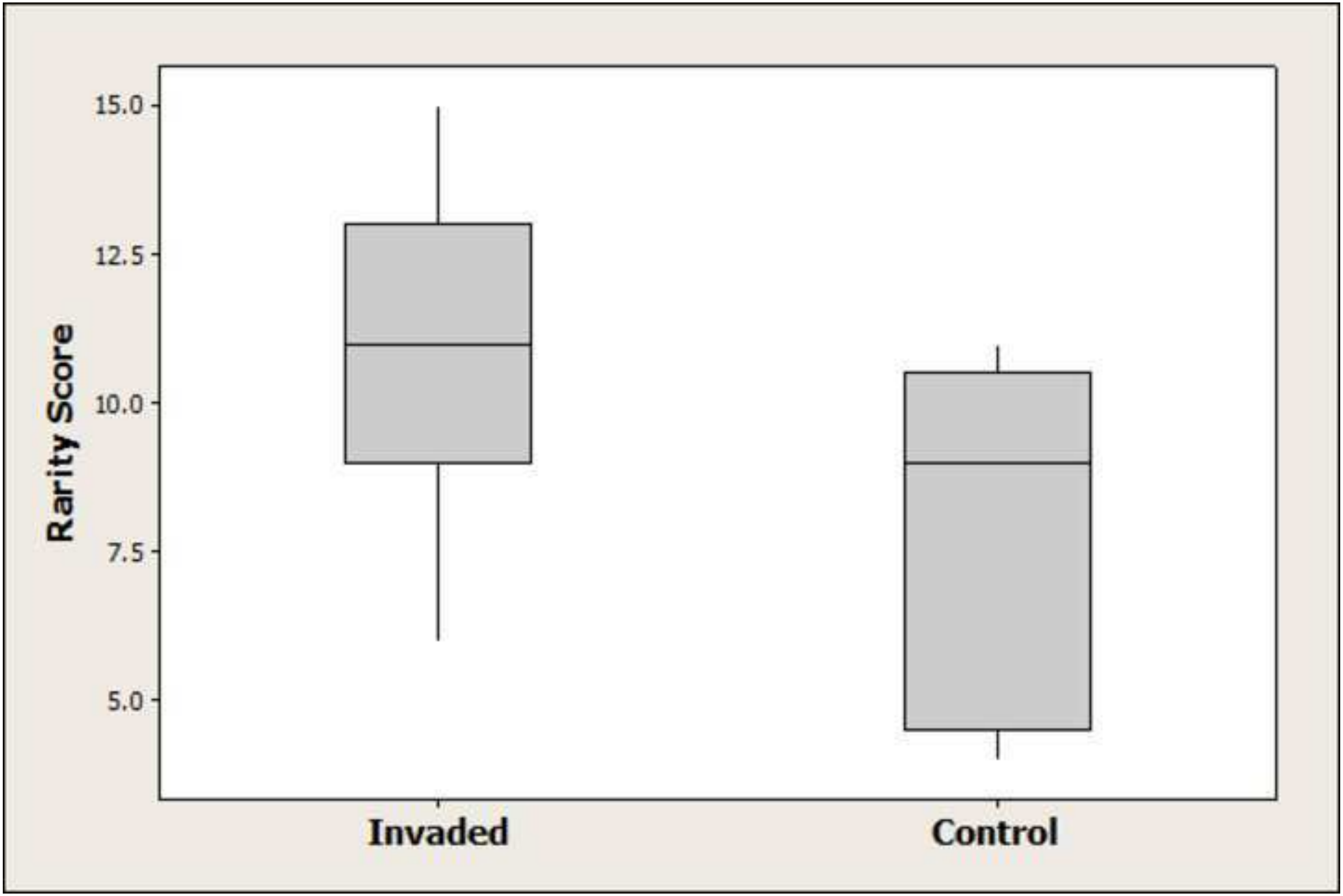
Black&White/ Grayscale figure
Click here to download Black&White/ Grayscale figure: Fig 2A BSBI total score coastal.tif



Black&White/ Grayscale figure
Click here to download Black&White/ Grayscale figure: Fig 2B 2010 total score coastal.tif



Black&White/ Grayscale figure
Click here to download Black&White/ Grayscale figure: Fig 2C PSYM total species number coastal.tif



Black&White/ Grayscale figure

Click here to download Black&White/ Grayscale figure: Fig 3 2010 average rarity score woodland.tif