The effects of future climate change on physiological traits and competitive abilities of invasive riparian plants Impatiens glandulifera and Heracleum mantegazzianum

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The effects of future climate change on physiological traits and competitive abilities of invasive riparian plants *Impatiens glandulifera* and *Heracleum mantegazzianum*

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ABSTRACT

Over the last few centuries, human activity has greatly contributed to different forms of global change, such as climate change and biological invasions, with great consequences for biodiversity and ecosystem services. The interactions between these factors need to be taken into consideration more carefully in order to better predict and mitigate negative impacts. Many recent studies have speculated about the possible effects of climate change on plant invasions. Riparian habitats have been repeatedly described in the literature as being highly susceptible to invasions by non-indigenous plant species. Due to the dynamic nature of rivers, it is likely that river systems will be very responsive to changing conditions, such as water temperature and altered hydrology. This thesis focuses on two of the most well-known and widespread riparian invasive species in Europe, *Impatiens glandulifera* Royle and *Heracleum mantegazzianum* Sommier & Levier.

I investigated the ways in which the performance and competitive abilities of these species might be affected by increased temperatures and climate-induced changes in soil moisture, respectively, as well as the future distributions of these species in Europe. Firstly, increased temperatures directly impacted the physiological and life-history traits of both invasive and native plants and, thus, competition outcomes for the invaded plant communities. Results suggested that warming might hinder invasion success in *I. glandulifera*, by quickening its life cycle and increasing growth of stems at the expense of biomass accumulation in roots and leaves, as well as by promoting the suppression of invader root growth by native species. Secondly, soil moisture seemed to have clear effects on the competition between *H. mantegazzianum* and co-occurring native species. Changes in soil moisture affected native species to a greater extent than the invader, increasing the community's susceptibility to invasion. Notably, excessive soil moisture experienced at the beginning of the growth season favoured invasion by *H. mantegazzianum* through reducing the native community's biomass, while simultaneously having little effect on the invader's biomass. However, drought conditions inhibited the growth and competitive abilities of *H. mantegazzianum* as well, even when biotic resistance from the native community was also low. Finally, species distribution models revealed that future warming could reduce the ranges of these species in Europe, as they shift northwards to Scandinavia and to higher altitudes. Nevertheless, as observations about competitive outcomes between invasive and co-occurring native species are highly context-dependent and can vary depending on the scale of the study and the species involved, it is crucial to examine multiple facets of these complex relationships. Riparian invasions could interact with other forms of global change in the near future in complex, species-specific and scale-dependent ways which need to be targeted by future researchers.

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CHAPTER 1

Literature Review - The potential effects of climate change on riparian plant invasions

1.1 INTRODUCTION

Over the last few centuries, human activity has facilitated the breakdown of geographic barriers which had separated the biotas of different continents for millions of years (Capinha *et al.*, 2015). Increasing global trade and travel contribute greatly to the movement of organisms around the globe and their introduction to regions far beyond their native ranges (Banks *et al.*, 2015; Chapman *et al.*, 2017). In these new regions, certain species can establish self-sustaining populations in the wild (i.e. naturalise) and disperse, thus becoming invasive (*sensu* Richardson *et al.*, 2000). Invasive species have been identified across all biological kingdoms, but vascular plants are some of the best documented in terms of distribution and history of spread (van Kleunen *et al.*, 2015). A great number of papers have reviewed the ecological, economic and social impacts invasive exotic plants are already having on indigenous biodiversity and ecosystem services (eg.: Levine *et al.*, 2003; Vila *et al.*, 2010; Pysek *et al.*, 2012).

Despite growing efforts, the accumulation rate of non-native species worldwide does not seem to be decreasing and attempts to control and eradicate invasive species have often had limited effectiveness (Seebens *et al.*, 2017). Policies have been implemented involving, on one hand, risk assessments of exotic species and the regulation of introduction pathways according to the predicted invasion risk, and, on the other hand, attempts at eradicating already existing invasive plant populations on site (McGeoch *et al.*, 2010). However, even though positive responses to these policies have been recorded, the signatory countries to the Convention on Biological Diversity (CBD) had still failed to reach the 2010 Biodiversity Target for the invasive alien species indicator of threat to biodiversity (McGeoch *et al.*, 2010). Consequently, it is becoming more and more important to consider the impact of invasions in concert with other forms of global change, in order to better mitigate them.

An increasing body of literature is addressing the question of whether climate change will affect biological invasion success in the future (Dukes and Mooney, 1999; Hellmann *et* al., 2008; Walther *et al.*, 2009). Certain studies, focused on vascular plants, suggest that recent climate alterations could already allow some introduced species to survive and persist in areas where temperature or water availability were previously critical limiting factors for their distribution (Dullinger *et al.*, 2016). However, invasion dynamics are often highly context-dependent, success being determined by complex interactions between factors such as human activity, habitat type, climate and the particular characteristics of native plant assemblages, as well as the ability of these plants to compete with non-native species

(González-Moreno *et al.*, 2014; Pysek *et al.*, 2010). Thus, it is important to examine the ways in which climate change might affect particular habitats and communities.

Ecologists have often suggested that some habitats might be more susceptible to invasions by exotic species than others; the most vulnerable being characterised by strong dispersal agents, frequent disturbance and high nutrient and water availability (Alpert *et al.*, 2000). Notably, river corridors have been repeatedly described as hotspots for exotic plant invasions, comparable to islands (Hood and Naiman, 2000; Pysek *et al.*, 2010). The dynamic nature of rivers plays a very important role in shaping riparian plant communities, through processes such as nutrient transport, propagule (seeds or vegetative fragments) dispersal and establishment, plant colonisation and succession, as well as the promotion of adaptive plant traits which ensure survival and growth under the variable environmental conditions and disturbance regimes which characterise these habitats (Camporeale *et al.*, 2013). Consequently, riverbank vegetation is likely to be very responsive to effects of climate change like warmer water temperatures and increased flood or drought risk, with possible consequences for the ability of native species to compete with non-native invasive plants (Rahel and Olden, 2008). It is necessary to consider the effects these changing conditions might have on the vulnerability of river corridors to plant invasions, as the restoration and conservation of these habitats is of great importance, due to their high biodiversity and the range of important ecosystem services they provide (Riis *et al.*, 2020).

The aim of this review is to offer some insight into the future of riparian plant invasions. I will initially examine the most important biotic and abiotic factors shaping the invasion patterns which can be currently observed in riparian habitats. Subsequently, I will discuss the potential ways in which these factors and, thus, invasion success, might be affected by two important variables which are predicted to alter under future climate change: temperature and river hydrology. To this end, I will propose a conceptual framework describing the potential links between these climate change-related variables and different aspects of plant invasions, as well as summarise experimental evidence from studies investigating these links. Finally, I will highlight priorities for further research, needed to fill gaps in current knowledge and contribute to efforts aimed at mitigating the impacts of plant invasions in river corridors under climate change.

1.2 FACTORS SHAPING CURRENT RIPARIAN PLANT INVASIONS

Riparian zones are the interfaces between terrestrial and freshwater ecosystems associated with rivers and streams, which are characterised by high degrees of dynamicity and complexity (Naiman and Decamps, 1997). They have highly diverse floras and provide important ecosystem services such as water purification, carbon sequestration, erosion control and regulation of the energy and material flow through the ecosystem (Riis *et al.*, 2020). However, the proper functioning of these habitats is currently under threat by degradation through changes in land-use, as well as biological invasions (Richardson *et al.*, 2007). A wide range of both abiotic and biotic factors have been put forward in the literature as being potentially important in determining a habitat's level of susceptibility to invasions (i.e. its invasibility), such as disturbance levels, resource availability, local biodiversity and biotic competition intensity (Alpert *et al.*, 2000). However, it is apparent in the literature that there are other key drivers of biological invasions. Firstly, the life-history traits of some introduced plants could allow them to be better invaders, by facilitating their spread (through a lower seed mass, for example) or improving their ability to compete for resources with native species (Hamilton *et al.*, 2006). Secondly, high propagule pressure (i.e. the number of non-native plants being introduced in a new region, usually through anthropogenic means) and rapid propagule transport have been shown to be essential for the successful establishment of invasive plant populations (Lockwood *et al.*, 2005). A special focus is placed in this review on the propagule pressure determined specifically by the water flow itself, as rivers often act as a mode of passive transport for plant propagules (Johansson *et al.*, 1996). It is likely, then, that habitat invasibility, invasiveness of introduced species and propagule pressure all act in concert in order to determine riparian invasion success (Lonsdale, 1999).

1.2.1 Habitat invasibility

There is a strong link between riparian vegetation and river flow regimes (Pettit *et al.*, 2001). Some of the most important abiotic factors often associated with the high invasibility of riparian zones are habitat heterogeneity and regular disturbance from flooding (Naiman *et al.*, 1993; Pollock *et al.*, 1998; Richardson *et al.,* 2007). Continuous erosion and deposition of sediment through these processes could provide opportunities for introduced plants to establish and spread (Pysek and Prach, 1993; Naiman and Decamps, 1997). The documented importance of these factors is consistent with the theory of fluctuating resource availability, according to which the susceptibility to invasion of a certain habitat depends on the availability and fluctuations in resources (Davis *et al.*, 2000). The theory postulates that non-native species can rapidly find opportunities to invade when resource supply increases abruptly in a community, due to the fact that the invaders no longer need to compete with native species for these resources that are usually limiting for them, such as light, water and nutrients. Furthermore, a characteristic of riparian habitats which could contribute to invasive species richness is their close contact with two distinct types of landscapes, which probably offers riparian plant communities a larger pool of both aquatic and terrestrial species they can draw from (Naiman and Decamps, 1997). It is important to note, however, that the abiotic factors promoting riparian plant invasions are often considered to be responsible for the high native species richness observed along river corridors as well (Naiman *et al.*, 1993; Pollock *et al.*, 1998; Richardson *et al.,* 2007).

In addition to growing conditions, the dynamics of plant invasions can, thus, also be shaped by biotic interactions. Charles Elton, the founder of invasion ecology, predicted in his seminal book "The Ecology of Invasions by Animals and Plants*"* that more diverse habitats should exhibit greater resistance to invasions, possibly due to the shortage of niche space available for introduced species to exploit (Elton, 1958). In support of this hypothesis, a meta-analysis by Levine *et al.* (2004) revealed that, in plant communities, high biodiversity can limit the abundance of invasive plants, which is consistent with findings from studies involving fluctuating resource levels (Maron and Marler, 2007). Nevertheless, studies on riparian invasions highlight a discrepancy between the diversity-invasibility theory and the abundance of riparian invasive plants, indicating that the relationship between invasive and native species richness is more complex and scale-dependent than originally hypothesised by Elton (Planty-Tabacchi *et al.*, 1996).

The discrepancy between expected and observed invasive plant abundance in riparian habitats could be attributed to fluctuations in resources and, consequently, competition intensity within the community. The extent to which native plants can outcompete invasive species and, thus, limit their spread could be restricted by the aforementioned pulses in resources which render competition less important in determining invasion success, regardless of native species richness (Stohlgren *et al.*, 1999). Furthermore, the previous presence of invasive plants in a patch of riparian habitat seems to promote further invasions, by creating instability in the habitat through the disruption or alteration of dynamic processes, such as sediment deposition patterns, and, thus, creating more niches for invasive plants to exploit (Pattison e*t al.*, 2018).

1.2.2 Invasiveness of exotic plants

Riparian invasions are likely to be also shaped by the invasiveness of exotic plants, determined by the intrinsic traits which allow them to invade river corridors (Alpert *et al.*, 2000). Whether certain performance-related traits have different values for invasive and non-invasive species, determining invasion success, is a contentious issue, with studies presenting contrasting results, depending on the scale of the studies and the species involved (Daehler, 2003; van Kleunen *et al.*, 2010). Nevertheless, some physiological characteristics have been frequently associated with invasive success and used in studies as indicators of invader performance and competitive abilities. For example, specific leaf area (i. e. the ratio between leaf area and leaf mass) is a major life-history trait which can offer important insights into the leaf economics of plants and, consequently, their capacity to conserve water and nutrients (which they might be competing for with other co-occurring species), sequester carbon and, ultimately, grow (Hamilton *et al.*, 2005). High specific leaf areas are correlated with rapid growth (Leishman *et al.*, 2009) and plant height is another central trait when discussing plant competition, especially in relation to light interception (Hamilton *et al.*, 2005). Biomass production is also often utilised in experiments as a way of assessing the level of invasion in a plant community (van Kleunen *et al.*, 2010; Duell *et al.*, 2021). Overall, evidence suggest that highly invasive plants tend to show greater values in traits related to high performance, such as growth rates, photosynthetic rates, water and nutrient use efficiency, specific leaf area, while also managing interactions and trade-offs between these different traits in accordance with environmental constraints (van Kleunen *et al.*, 2010).

In the case of riparian habitats, there is evidence to suggest that widespread riparian invaders could owe their success not to inherently greater competitive abilities and growth rates than those of native species, but to a relatively superior ability to capitalise on the highly variable conditions present in these habitats (Daehler, 2003). It is likely that many invasive plants exhibit greater phenotypic plasticity than co-occurring natives, which allows them to occupy a wider variety of niches, especially in frequently disturbed habitats (Richards *et al.*, 2006; Dawson *et al.*, 2012; Parepa *et al.*, 2013). Additionally, fast dispersing species are generally considered to be more invasive, making use of traits such as small seed size and high seed number and viability (Alpert *et al.*, 2000). However, intrinsic dispersion rates might be less important for riverbank vegetation, as passive transport by water streams plays a great role in seed dispersal. However, competitive abilities could become more important in the context of climate change, especially if resource availability decreases in some areas and competition with natives intensifies, becoming a greater limiting factor in the spread of invasive species.

1.2.3 Propagule pressure and transport

Even if a habitat is considered to be highly susceptible to invasions and the introduced plant possesses traits which facilitate its establishment in the new environment, strong propagule pressure is still necessary for a high degree of invasion (Guo *et al.*, 2015). Plant invasions might be promoted through the passive transport of propagules (seeds, vegetative parts) by water along river corridors through hydrochory, an important process involved in shaping riparian vegetation (Johansson *et al.*, 1996; Jansson *et al.*, 2005; Nilsson *et al.*, 2010). Hydrochory could help non-indigenous plants overcome the limits imposed by their own dispersal abilities in various climates, as illustrated by Lonsdale (1993), examining the woody weed *Mimosa pigra* in northern Australia, or Thebaud and Debussche (1991), in their study on the invasive tree *Fraxinus ornus* in southern France. It is, thus, important to discuss the way in which invasibility, invasiveness and propagule pressure might be differentially affected by various aspects of future climate change.

1.3 RIPARIAN PLANT INVASIONS IN A CHANGING CLIMATE

Climate change is considered one of the greatest threats to ecosystems and biodiversity worldwide (IPBES, 2019). Future increased temperatures and changes in precipitation patterns have been predicted to greatly impact many aspects of river hydrology and, consequently, riparian vegetation (Capon *et al.*, 2013). These changes do not seem to be unidirectional or uniform, with strong regional trends already being observable (IPCC, 2014). For example, in Europe, recent climate change has led to reduced floods in southeastern countries, while the Northeast has seen an increase in flooding (Christensen and Christensen, 2007; Blöschl *et al.*, 2019). This pattern of decreased water-flow in more arid riparian habitats has also been predicted in south-western US, particularly in the San Pedro Basin (Serrat-Capdevila *et al.*, 2007). Increased climate variability might also lead to a higher frequency of extreme events, such as storms and hurricanes (Katz and Brown, 1992). Additionally, the timings of seasonal variations in water-table levels may differ due to altered rainfall patterns (Capon *et al.*, 2013). It is important to note, however, that the influence of local precipitation on flooding patterns might be dependent on the size of the watershed, diminishing with increasing size (Junk *et al.*, 1989). Nevertheless, such altered abiotic conditions under climate change are very likely to affect plant invasion dynamics along river corridors and they might act differentially on the different processes involved in invasions described in the previous section (Figure 1.1).

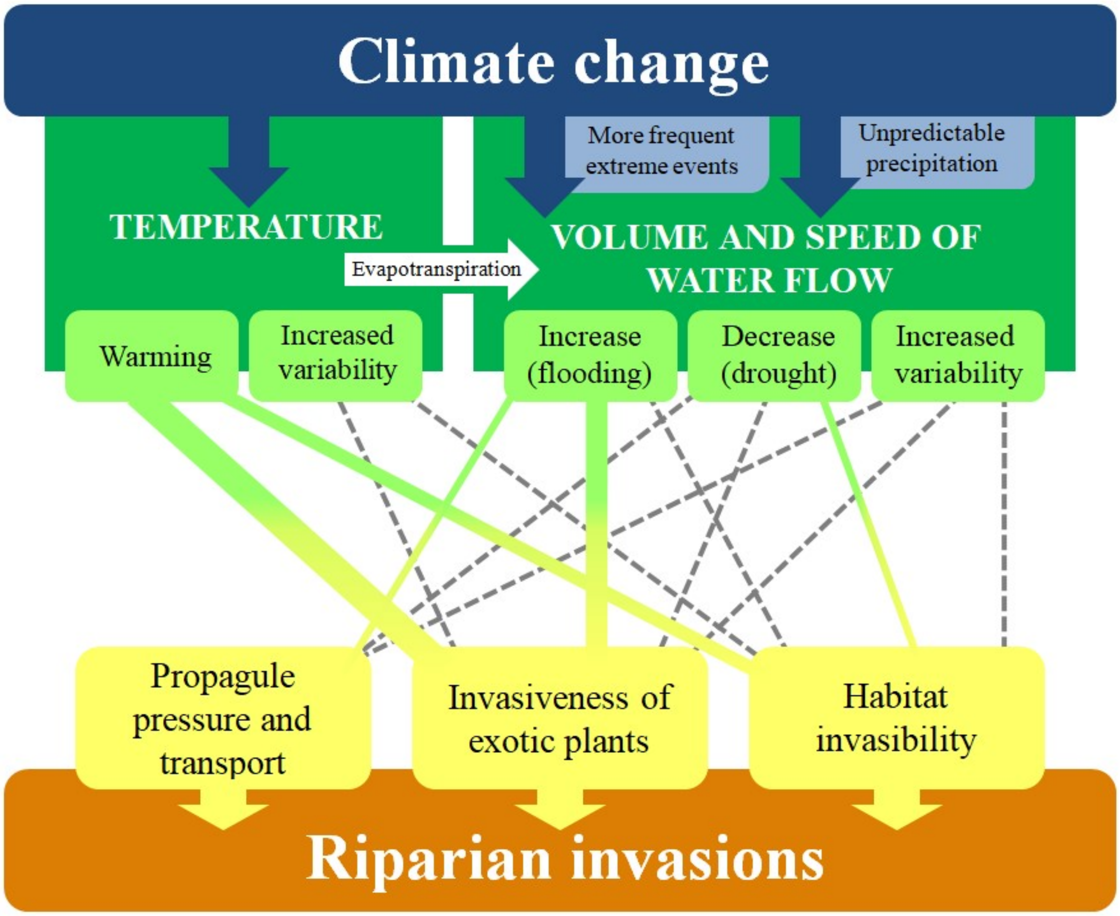

Figure 1.1. Conceptual framework highlighting the possible links between climate change variables and different aspects of plant invasions. The dotted lines indicate links for which no experimental studies were identified during the literature search detailed in Table 1.1, but which are the results of speculation based on other studies cited in the text. The thickness of the continuous lines is proportional to the number of experimental studies investigating the link identified during the same search.

It has been postulated that invasive species have relatively broader environmental tolerances (possibly as a result of phenotypic plasticity), whereas many native riparian species seem to be habitat specialists well adapted to surviving in the highly variable conditions of riverbanks (Naiman and Decamps, 1997; Richardson et al, 2007). Models suggest that specialists are more constrained by their present conditions and are less likely to cope well with future environmental changes (Evangelista *et al.*, 2008). Thus, riparian plant communities face the risk of becoming even more vulnerable to invasion, as their increased invasibility could allow for more plastic exotic plants to establish. Nonetheless, Hellmann *et al.* (2008) predicted that climate change could impact the invasive abilities of introduced species, and the life-history traits and physiological parameters underpinning them, at all stages of the invasion process.

Predictive models, including ones which incorporate the understanding of geo-ecological processes at fine spatial resolutions (Murray *et al.*, 2012), point towards changes in habitat suitability and range shifts in many freshwater invasive plants (Beerling, 1993). Consequently, some plants which were already invasive in an area could be allowed to spread even further in these new conditions, while some previously benign introduced plants could become invasive. A number of mechanisms could support these changes, including phenology shifts in these exotic plants, which they appear to undergo more easily in response to climatic alterations than native species (Willis *et al.*, 2010; Wolkovich *et al.*, 2013; Keller and Shea, 2021). Furthermore, it is possible that climate change will reduce resource supply or the frequency of resource pulses in riparian habitats at particular times, leading to more intense competition between already established species. The outcomes of these altered interactions and their implications for invasion success are difficult to predict, as resource scarcity can also impact the fitness of native plants and cause them to become less vigorous competitors under changing environmental conditions. For example, reduced summer run-off due to higher temperatures can lead to both increased drought stress on native plants, as well as a greater need to compete for water with exotic species, with possible negative impacts for native plant diversity and abundance (Rood *et al.*, 2008). However, there is limited experimental evidence investigating the links between changes in temperature and precipitation and various facets of riparian plant invasions. I will follow the focus of research into climate change impacts and summarise key findings of experimental studies which have investigated the effects of warmer temperatures and changing hydrological processes on invasions (Table 1.1).

Table 1.1. Complete list of results of a systematic literature search targeted at identifying experimental evidence directly linking riparian and wetland plant invasions and climate change. The search was conducted on the Web of Science core collection database on February 15th 2021 and papers were manually screened for inclusion or exclusion at title and abstract level.

Invasion element	**Climate variable**	**Effect**	**Type**	**Reference (Location)**
INVASIBILITY	Temperature	Decreased invasive species richness and productivity in warmer waters	Field	Flanagan *et al.*, 2015 (USA)
		Native plant mass reduced by warming; no effect on non-native plant mass	Field	Meza-Lopez and Siemann, 2020 (USA)
	Hydrology	Native species performance more hindered by aridity than invasive performance	Pots	Perry *et al.*, 2012 (USA)
INVASIVENESS	Temperature	Invasive plant germination and biomass increased, but germinant survivorship decreased by warming	Pots	Gillard *et al.*, 2017a (USA/France)
		Invasive plant germination stimulated by elevated temperatures	Pots	Gillard *et al.*, 2017b (USA/France)
		Germination and bud-break inhibited due to insufficient chilling	Field	Guilbault *et al*, 2012 (USA)
		Differential responses to warming of two haplotypes: smaller leaves and increased stomatal conductance and transpiration in one case, lower carboxylation and electron transport rates in the other	Pots	Prince *et al.*, 2018 (USA)
	Hydrology	Higher biomass of invasive plants in flooding conditions, with negative or absent effects on natives	Field	Wang *et al.*, 2015 (China)
		Higher nutrient release and uptake rates for invasive species than natives in flooding conditions	Field	Wang *et al.*, 2018 (China)
		Invasive plant growth inhibited by submergence	Pots	Zhang *et al.*, 2016 (China)
PROPAGULE PRESSURE	Hydrology	Invasive plant dispersal promoted by river high-flow events	Pots	Truscott *et al.*, 2006 (UK)

1.3.1 Temperature

Previous findings from natural, field and indoor growth experiments reveal that increased temperatures do not show clear direct effects on the success of riparian plant invasions, despite it being one of the best studied links proposed in the conceptual framework previously presented (Figure 1.1). A study centred on a natural experiment in US wetlands showed that climatic variables have a much stronger effect on the abundance of native species compared to invasive ones, the latter being influenced by more site-specific variables, such as nutrient availability and land use (Flanagan *et al.*, 2015), which is consistent with the resource fluctuation theory discussed in the previous section. The same paper suggested that local natives had an advantage at sites with warmer waters, as most of the important invasive plants present in the area originated from higher latitudes. Similarly, plants which require low spring temperatures for germination and bud-break, such as the Russian olive *Elaeagnus angustifolia*, might become increasingly limited in range due to warming climate trends (Guilbault *et al.*, 2012). In contrast, invasive plants from Oceanic climates, such as water primroses (*Ludwigia* spp.), might see an increase in invasiveness due to warming stimulating germination and biomass production (Gillard *et al.*, 2017a; Gillard *et al.*, 2017b). Furthermore, Meza-Lopez and Siemann (2020) have described an increase in native community invasibility with warmer temperatures, as native biomass was reduced, but no effects were observed on invasive species' growth. Thus, the provenance of the invasive species, as well as the vulnerability of the co-occurring natives to warmer temperatures, could play an important role when determining the impacts of climate change on riparian invasions.

Despite the fact that direct impacts seem limited and difficult to interpret, there are also some indirect effects of warming on riparian plant invasions which are worth mentioning. For instance, elevated temperatures and CO_2 concentrations have been shown to promote herbicide resistance in *Phragmites australis*, as a result of decreased herbicide uptake into leaves with smaller areas determined by heat stress (Prince *et al.*, 2018). In addition, higher temperatures could lead to modified interactions between plants and herbivores, and, thus, herbivorous insects used as biological control agents (Lu *et al.*, 2013). These insects might become less effective in controlling invasive species, while having greater negative impacts on non-target native species in a warmer climate (Lu *et al.*, 2014).

1.3.2 Hydrology

It is apparent that river hydrology is the most important driving force structuring plant communities in riparian zones (Naiman and Decamps, 1997). When attempting to gain insight into the future of plant invasions in these habitats, it is important to consider the effects of water as both a readily available resource and as a source of regular disturbance. In regards to water as a resource, variation in soil moisture seems to have a great influence on riparian vegetation (Tickner *et al.*, 2001). A reason for this might be the different rooting strategies plants need to adopt in order to cope with this variation (Tickner *et al.*, 2001). In areas where water availability is predicted to increase, plant invasions could be favoured due to the opportunistic water-use which characterises many successful invaders (Dawson *et al.*, 2012). On the other hand, the impacts of reduced water availability and more frequent droughts might heavily depend on the drought-tolerance and water-use abilities of each particular invasive plant species. (Perry *et al.*, 2012). Information found in the literature seems somewhat contradictory in regards to this, as Zavaleta (2000) postulated that *Tamarix* spp. use more water than co-occurring natives, while Perry *et al.* (2012) found that *Tamarix* spp. coped better with low water availability than the natives studied. It might then be useful to consider how decreases in river run-off have the potential to increase salinity in riparian soils, which can lead to the loss of native species and spread of exotic plants which have higher tolerances to such conditions (An *et al.*, 2002). For instance, in Southwestern US, the invasive saltcedar (*Tamarix ramosissima*) was found to be more tolerant to increased river salinity than the native cottonwood (*Populus fremontii*), albeit marginally (Shafroth *et al.,* 1995). Additionally, even if increased salinity affects invasive plant growth as well, the elevated temperatures and CO_2 concentrations associated with climate change may help alleviate its negative effects (Eller *et al.*, 2013). Lower water tables could also expose bare areas which provide invasive species with more opportunities for germination, as shown in the case of the common reed *Phragmites australis* in Canada (Tougas-Tellier *et al.*, 2015). Furthermore, the effects of drought on plant invasions can also be indirect. For example, Kane *et al.* (2011) found that in a *Juniperus monosperma* woodland in Arizona, where climate change-induced droughts were increasing the mortality of junipers, the invasive cheatgrass *Bromus tectorum* was more abundant when growing under dead junipers than under living ones.

A different mechanism through which generally increased water tables might affect invasion success on river margins is disturbance through flooding. Climate change could alter the frequency, intensity and variability of flooding events. Ecologists have hypothesised that invasive potential in areas such as riparian habitats and wetlands is strongly related to the flood-tolerance of introduced species, with successful invaders being more tolerant than co-occurring natives and, thus, being able to take advantage of increased habitat invasibility (Kercher and Zedler, 2004). Besides the increased disturbance and enhanced dispersal of invasive plant propagules associated with a higher occurrence of high-flow events (Truscott *et al.*, 2016), flooding might promote invasions through alterations in soil composition and nutrient content. In the Minjiang River estuary in China, flooding was shown to alter nitrogen and carbon plant-soil cycles, with the invasive *Phragmites australis* taking up significantly more carbon and nitrogen in flooding conditions than either of the native species studied (Wang *et al.*, 2015). Furthermore, invasive plants benefited from a better nutrient supply during the growth season due to increased litter decomposition facilitated by higher flooding intensity, gaining a competitive advantage over indigenous species (Wang *et al.*, 2018). Nevertheless, although invasive plant growth has been shown to be promoted by more frequent and intense flooding events, continued submergence may prove to be detrimental in terms of invasiveness. Individuals of the widespread invasive riparian plant *Alternanthera philoxeroides* subjected to submergence suffered severe growth inhibition, despite the fact that they displayed phenotypic plasticity by lengthening their stems (Zhang *et al.*, 2016).

Moreover, submergence could lead to the deposition of sediment on leaves, which inhibits photosynthesis (Tickner *et al.*, 2001).

Finally, there are other possible effects of climate change on river hydrology than unidirectional changes in water volume and speed. Firstly, there could be changes in variability and seasonality in stream flow dynamics (Capon *et al.*, 2013). Timings of flooding events might be extremely important in plant growth in riparian zones and changes could lead to phenological mismatching for these plants, as well as various ramifications for plant invasions (Tickner *et al.*, 2001). For example, a more variable water-flow has been shown to increase the cover of *I. glandulifera* along UK riverbanks (Pattison *et al.*, 2018). However, more experiments need to be carried out with the target of understanding the relationship between hydroperiod and invasion dynamics along river corridors. Secondly, extreme weather events could become more frequent and have a great impact on riparian vegetation structure (Katz and Brown, 1992). Tropical storm and hurricane activity over the past several decades explained most of the variation in *Phragmites australis* growth in a large area of US wetlands (Bhattarai and Cronin, 2014). Thus, it is likely that increases in the frequency and intensity of extreme events predicted for the end of the century and the resulting disturbances might stimulate the spread of invasive plants.

1.4 CONCLUSIONS AND FUTURE DIRECTIONS FOR RESEARCH

Although many papers have been written about the dynamics of riparian habitats under future climate change scenarios, particularly in relation to water regulation systems and restoration strategies, few pay attention to invasions in particular. The evidence summarised in this review suggests that future climate change could have a great impact on plant invasion success in riparian habitats, by altering both the abiotic and biotic constraints which together shape patterns of invasion. These findings are consistent with models predicting novel riparian ecosystems under climate change, characterised by reduced native biodiversity and an increased spread of non-native invasive species (Catford *et al.*, 2013). While the effects of temperature on invasion success might vary depending on the responses of natives and the ability of invasives to capitalise on such responses if they are negative, the impacts of river hydrology seem much more central in determining the future of exotic plants on river margins. Higher frequency and intensity of flooding events, increases in salinity due to decreased water levels, extreme events and more variable flow patterns could all provide disturbances which have the potential to promote riparian plant invasions success. Disturbance has also been linked to the resource fluctuation theory discussed earlier in this review, with evidence showing that competition between native and invasive plants can become less intense after disturbance events that increase resource availability and, thus, promote invaders (Davis *et al.*, 2000). However, prolonged floods and submergence seem to inhibit invader growth alongside native species, and a climate-induced scarcity of resources could intensify competition and provide an opportunity for diverse riparian plant communities to limit some introductions and invasions.

The limitations to the conclusions we can draw given the current literature indicate the need for more robust evidence and separation of the many factors acting upon both non-native and indigenous species. Many studies have assessed and compared the performance of co-occurring native and invasive plant species, by measuring a range of physiological parameters in various growing conditions and across different life forms, in order to determine the traits and circumstances which allow successful invaders to outcompete indigenous species (see review by Daehler, 2003). However, there is a scarcity of experimental studies comparing these performances under future climate change scenarios explicitly. The higher number of experiments investigating exotic plant invasiveness rather than habitat invasibility might be a consequence of the fact that the majority of these studies focus on the performance of invasive species under various treatments and rarely consider communities in their entirety, taking into account biotic resistance and competition effects. Studies combining bioclimatic modelling approaches and subsequent ground-truthing by means of manipulative experiments might provide a more complete picture of invasion patterns under climate change. Furthermore, most of the available research is limited to the United States, Western Europe and China. It might be useful to include in the available body of literature studies investigating river systems from other parts of the world as well, as they might exhibit different predicted patterns of precipitation than the ones described in this review. Finally, there is a need for further research into the relationship between extreme weather events, as well as extreme temperatures, and invader success in riparian zones.

In conclusion, it is important to take into consideration the particular challenges faced by plants in certain types of habitats when trying to predict dynamics and effects of plants invasions under climate change. Thus, Chapters 2 and 3 each focus on the physiological responses of two invasive plant species widely spread throughout UK and western European river catchments, *Impatiens glandulifera* Royle (family Balsaminaceae; Gilman, 2015) and *Heracleum mantegazzianum* Sommier & Levier (family Apiaceae; Gilman, 2015), to changes in temperature and soil moisture, respectively, in order to determine the specific effects climate change might have on their local success in the future. Assigning one invasive species to each of the two experiments was done for primarily pragmatic reasons. Firstly, the limited space available in the growth chamber used for the temperature experiment did not allow for the inclusion of both species, while still maintaining a high number of replicates. Thus, *I. glandulifera* was chosen for this experiment, as it is a less strictly riparian plant than *H. mantegazzianum*, which was prioritised as a species for the watering experiment. Secondly, both species were used in the water experiment, but, as my project was carried out in collaboration with another Research Masters project student, the workload was split and the present thesis only discusses the soil moisture experiment in relation to *H. mantegazzianum*.

Despite the possible effects of climate change described in this review, disturbance driven by changes in land use, eutrophication, habitat destruction and fragmentation or the existence of flow regulation systems, such as dams, still has a great influence on the composition and functioning of riparian vegetation, as well as the invasion patterns observed in these habitats (Miller and Zedler, 2003; Murray *et al*., 2012). One of the greatest challenges to the management of plant invasions along river corridors in the future will probably be the integration of these different forms of global change in management strategies by evaluating and attempting to mitigate anthropogenic effects on hydrological regimes and structural habitat integrity in a warming, increasingly unpredictable climate.

CHAPTER 2

How will rising temperatures affect the competitive abilities of the riparian invader *Impatiens glandulifera*?

2.1 INTRODUCTION

Continued emissions of anthropogenic greenhouse gases into the Earth's atmosphere have been predicted to lead to an increase in the global mean surface temperature of 0.3-4.8°C by the end of this century (IPCC, 2014). Additionally, climate change could lead to more frequent and intense heat waves (Meehl and Tebaldi, 2004), which have already been observed in recent years (Easterling *et al.*, 2000). Both modelling approaches and experimental studies have shown that changing environmental conditions have already impacted plant physiology, growth and survival (Allen *et al.,* 2010; Becklin *et al.*, 2016), and will most likely continue to affect plant performance in a warmer future (Harte and Shaw, 1995). As these responses vary greatly between co-occurring species and they play a great role in plant-plant interactions and competition outcomes (Brooker, 2006), climate change has a great potential to alter plant community structures in many ecosystems and habitats (Weltzin *et al.*, 2003; Williams *et al.*, 2007). Of particular note in this regard are the possible effects higher temperatures might have on the introduction and establishment of non-native species and, thus, plant invasion dynamics (Bradley *et al.*, 2010). Invasive plants could become a greater threat, with climate change adding another layer of complexity to management planning and predicting the future functioning of ecosystems (Walther *et al.*, 2009).

In the past few decades, ecologists have hypothesised that global warming will allow certain invasive species to be introduced, spread and establish into areas where lower temperatures were previously a limiting factor (Walther *et al.*, 2009; Dullinger *et al.*, 2016). In already invaded habitats, changes in environmental conditions can also lead to more or less intense competition between native and invasive species, depending on whether resources become more abundant (decreased competition) or scarce (increased competition; see Chapter 1). However, the potential effects of increasing temperatures on the intrinsic ability of invasive plants to outcompete co-occurring native species (i.e. their invasiveness) after they are already established remain poorly understood. Invasiveness has been associated with a variety of physiological and life-history plant traits (McDowell, 2002; Daehler, 2003; van Kleunen *et al.*, 2010). Existing literature indicates that both increased temperatures and extreme heating events can have significant, but mixed, effects on some of these traits, such as growth rates, germination capacity, biomass allocation patterns, leaf economics, carbon capture strategies and chemical defences (Song *et al.*, 2010; Verlinden and Nijs, 2010; Wang *et al.*, 2011; Hou *et al.*, 2014; Gillard *et al.*, 2017a; Gillard *et al.*, 2017b; Keller and Shea, 2021). For example, invasive plants which are tall and have high specific leaf areas, photosynthetic rates and biomass accumulation capacities are considered more likely to be better competitors and withstand biotic resistance from indigenous plant assemblages (Hamilton *et al.*, 2005; van Kleunen *et al.*, 2010).

Increased temperatures can bring about changes in all of the aforementioned plant traits and, as a consequence, affect competition and non-native plant success in invaded habitats. Invasive species growth can be promoted by warmer conditions (Gillard *et al.*, 2017a), but it is also possible that native growth rates and biomass can be reduced by increased temperatures, with no effects on co-occurring invasive species, which increases the proportion of invader within the community and, thus, its invasion success (Meza-Lopez and Siemann, 2020). Competition outcomes for native and invasive species can also be determined by each species' ability to withstand heat stress at leaf level. Prince *et al.* (2018) suggests that climate can have less of an effect on the specific leaf-area (SLA), carboxylation, transpiration and stomatal conductance rates of the *Phragmites australis* invaded range haplotype than on the native range one, with consequences for growth and chemical uptake. The invasive plant *Wedelia trilobata* has been shown to have greater thermostability of its photosynthetic apparatus and to suffer less inhibition of net photosynthetic rates and biomass production due to higher temperatures than its indigenous congener *Wedelia chinensis* (Song *et al.*, 2010). This finding is consistent with the aforementioned results of Meza-Lopez and Siemann (2020) and highlights the importance of understanding the leaf processes that underpin observed effects of temperature on growth.

It is also important to consider root-level effects on competitive outcomes, as proper and efficient root development is essential for nutrient uptake and can dictate competitive success when nutrients are limited (McCormack and Iversen, 2019). In particular, specific root length (SRL) can be considered the equivalent of SLA when discussing root economics (Withington *et al.*, 2006). However, though it is possible that, like SLA, SRL might change in response to higher temperatures in ways which can aid or hinder invasive plants in competing with co-occurring native species, it is much less clear in the literature what trends SRL follows in response to environmental changes and stress (Ostonen *et al.*, 2007). The role of phenotypic plasticity and phenological shifts should also not be overlooked, as invasive plant species have been shown to be more likely to alter their life cycle in order to more closely track climate change than native species growing in similar conditions (Daehler, 2003; Wolkovich *et al.*, 2013; Keller and Shea, 2021).

There is evidence to suggest that some of the traits linked with invasiveness are not fundamentally different from the traits of native species, but are rather better supported in certain growing conditions, like habitats characterised by high resource availability and frequent disturbance (Daehler, 2003; Leishman *et al.*, 2009). Important examples of such habitats are riparian zones, the transition areas between terrestrial and freshwater ecosystems (Naiman and Decamps, 1997). Riparian habitats have a great importance in terms of biodiversity and ecosystem services, but they have also been put forward as not only more likely to be severely impacted by climate change, but also as more vulnerable to biological invasions (Capon *et al.*, 2013). Consequently, predicting the future of plant invasions in riparian habitats in a warming climate might prove to be particularly challenging. One of the most important riparian invasive plant species in Europe, with a long history of invasion in UK river catchments, is *Impatiens glandulifera* Royle (Gilman, 2015) – Himalayan Balsam (Pysek and Prach, 1995). The negative effects of *I. glandulifera* on the biodiversity and functioning of invaded communities in the UK have been repeatedly documented (Hulme and Bremner, 2005; Tanner *et al.*, 2013). In Northwestern Europe, studies have suggested that temperature is an important limiting factor in the distribution of *I. glandulifera* and that further spread to higher latitudes is likely (Beerling, 1993; Willis and Hulme, 2002). Thus, it is vital to understand how the performance of this species might be affected by future climate change, in order to better manage invader populations and limit the damage suffered by vulnerable riparian habitats.

There is a scarcity of manipulative experiments investigating the effects of increasing temperatures on the intrinsic competitive abilities of certain non-native plant species, despite the fact that the results of this type of experiment are usually more consistent than other approaches of studying plant tolerances to warming (Elmendorf *et al.*, 2015). The present experiment explores physiological traits which have been linked to plant performance and invasion success - growth, biomass allocation, specific leaf area, specific root length, net photosynthesis, dark respiration, stomatal conductance and transpiration – in an annual non-native species, *I. glandulifera,* in the context of future climate change. Firstly, I investigated whether these parameters differ between plants grown in an artificial environment simulating current temperatures in County Durham, UK, and one reflecting warmer temperatures projected for the end of the century. Secondly, I considered the ways in which responses to climate change might differ between *I. glandulifera* individuals participating in either interspecific or intraspecific competition. Finally, the performance of co-occurring perennial native species was also assessed in order to reach a better understanding of alternative strategies plants might adopt in response to climate warming.

2.2 METHODS

2.2.1 Study species and seed preparation

In this experiment, I focused on one of the most well-known and widespread invasive plant species in Europe: *Impatiens glandulifera* Royle (family Balsaminaceae). Alongside *I. glandulifera*, three other vascular plant species which are common throughout the UK were used in order to simulate a native riparian plant community: *Epilobium hirsutum* L. (Gilman, 2015), *Jacobaea vulgaris* Gaertn. (Kozhevnikov *et al.*, 2019) and *Silene dioica* L. (Gilman, 2015). The three native species, all perennials, were chosen because they were readily available, as well as the fact that they germinate easily and occur in the same habitats as *I.*

glandulifera in County Durham. Wild populations found in and around Durham City, County Durham, along the river Wear, were used to obtain seeds for *I. glandulifera* (54.7714 N, 1.5550 W; 54.7761 N, 1.5783 W; 54.7731 N, 1.5728 W; 54.7764 N, 1.5687 W), *E. hirsutum* (54.7764 N, 1.5675 W), *J. vulgaris* (54.7764 N, 1.5675 W) and *S. dioica* (54.7711 N, 1.5593 W). A variety of locations were chosen for the collection of *I. glandulifera* seeds in order to obtain a range of genotypes and maximise the chances of germination. Over a period of 3 months, *I. glandulifera* seeds were subjected to cold stratification in wet sand, at 4°C, in order to break dormancy and stimulate germination. Subsequently, seeds from all natives and *I. glandulifera* were sown on moist sand and allowed to germinate and grow for 4 weeks (January 13th to February 10th, 2021) in a greenhouse setting (21°C, ambient lighting) before transplanting.

2.2.2 Growth chambers set-up

The manipulative growth experiment entailed the simulation of rising temperatures under climate change and was carried out over a 9-week period (February 10th to April 14th, 2021). The native and invasive plants were grown in two controlled growth chambers, one reflecting the current UK climate, while the other emulated conditions associated with future climate warming. The climatic regime in the first chamber was determined through an analysis of hourly temperature and humidity for May and June in Durham, between 2010 and 2020. In the second growth chamber, the temperature was set to 3°C higher, in line with the results of probabilistic predictions for future temperature in North East England under the higher emission climate change scenarios described in the UKCP18 Report (Met Office, 2018). Consequently, temperatures in the present climate chamber ranged between 10-18.5°C, whilst the future climate had temperatures between 13-21.5°C (Figure 2.1). Furthermore, the light regime in both chambers mimicked the day-night cycle characteristic for the month of May in Durham: light between 05:00-21:00, dark between 21:30-04:30, and dimmed lights (simulating twilight; 50 μmoles/m^2/s) in the 04:30-05:00 and 21:00-21:30 intervals. Light intensity values were measured at plant height and were chosen in order to approximate natural light intensity on overcast days (Garnham, 1999), which were frequent in Durham City at the time the experiment was carried out. Initially, the daytime light intensity was set at 150 μmoles/m^2/s, so as to not expose the seedlings to excessive light intensity levels too early. However, halfway through the experiment, during week 5, daytime light intensity was increased to 500 μmoles/m^2/s.

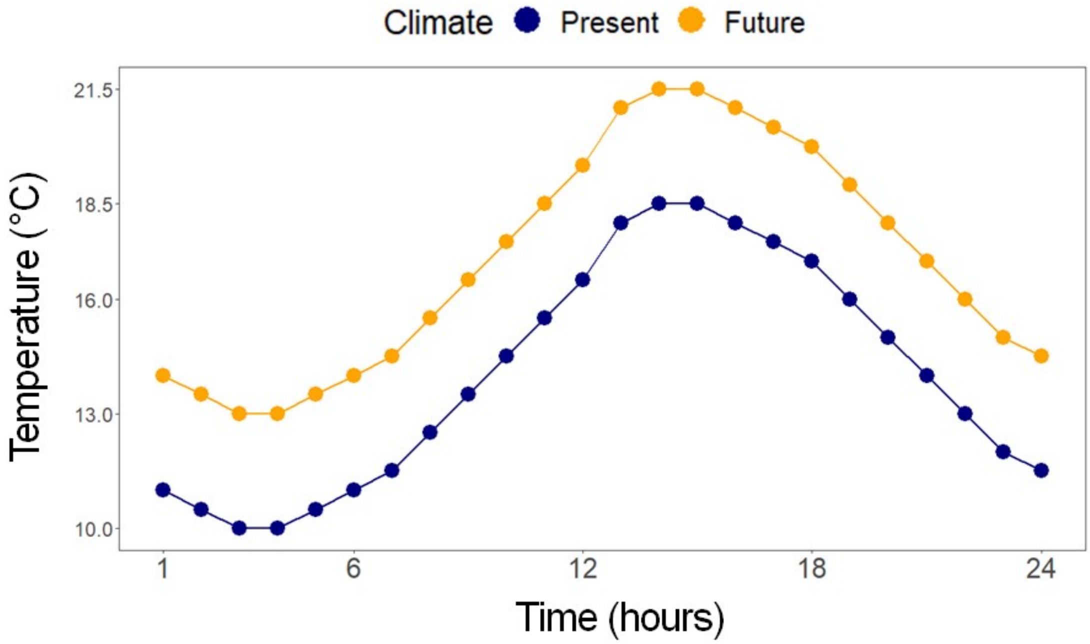

Figure 2.1. Daily temperature regimes in the two growth chambers

Each growth chamber had internal dimensions of 1.2 m x 0.75 m and contained 40 plant pots, placed approximately 5 cm apart from each other. The total number of 80 pots was split into four categories as follows: 20 pots containing only *I. glandulifera* individuals, 20 pots containing native communities consisting of only the three aforementioned riparian species, 20 pots where native plants were grown together with *I. glandulifera*, and 20 control pots exclusively containing soil. The control pots were set for future use in a follow-up experiment by a colleague. Each set of 20 pots was split into two, with half being assigned to the current climate chamber and the other half to the future climate chamber (Table 2.1). Pots were randomised within the chambers. At the halfway point of the experiment, both the temperature settings and the pots (maintaining the same randomized distribution they had in the previous chamber) were swapped between the two chambers. This was done in order to account for any confounding effects related to the chambers themselves.

Table 2.1. Number of pots allocated to each type of community under each temperature treatment

Community composition	**Growth chamber**	
	Current climate	**Future climate**
I. glandulifera (I)	10	10
Native (C)	10	10
Native + *I. glandulifera* (CI)	10	10
Control	10	10

The pots used in this experiment each had a 10.5 cm diameter, 13 cm height and 1 L capacity. They were filled with 1 L of a 2:1 mixture of sterilised sand and soil collected around Durham, from 10 different areas which had not previously been invaded by *I. glandulifera*. Each set of 8 pots (Table 2.1) was filled with soil from the same sample. In pots with soil originating from the same location, the central *I. glandulifera* seedlings, in both CI and I pots, were grown from seeds collected from the same plant (siblings). In this way, confounding effects related to both genetic variation and differences in soil microbiota were reduced. Where possible, I used seedlings showing at least one pair of true leaves (i.e. excluding cotyledons). Seedlings were planted 1 cm below the soil surface. 40 pots contained an individual seedling from each of the native species and, additionally, an *I. glandulifera* seedling was added to the middle of 20 of these pots. Finally, in the pots containing only *I. glandulifera*, 3 seedlings were planted (Figure 2.2). Consequently, I and C pots contained three seedlings each, while CI pots contained four. It was not possible to realise equal plant densities in community types, due to practical constraints related to the aforementioned parallel experiment carried out by another Research Master's student, which required that C and I pots contain the same number of plants.

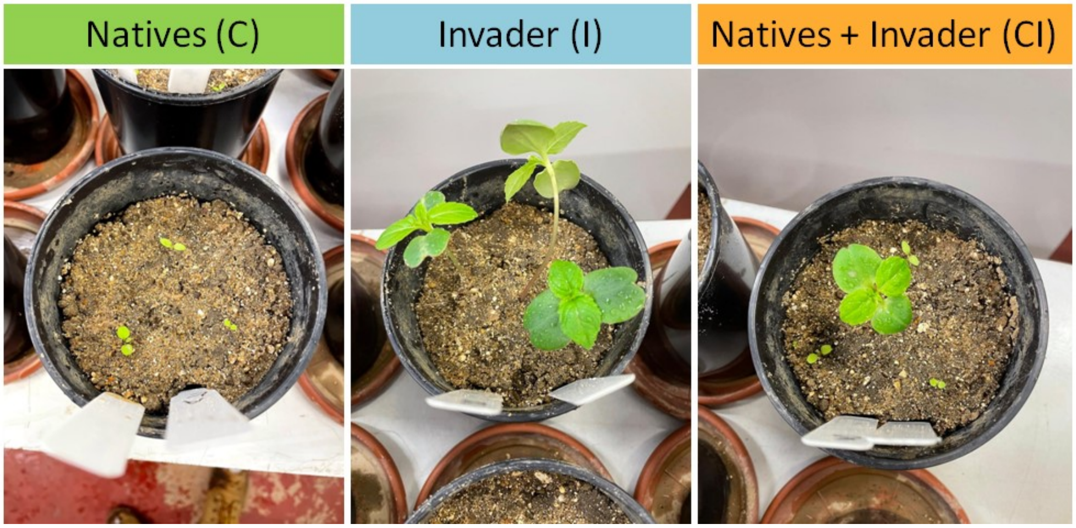

Figure 2.2. The three types of experimental communities, shortly before the pots were placed in the growth chambers

The growing plants were initially watered twice a week, using a total quantity of 100 ml distilled water per week (50 ml, twice a week), which was increased to 150 ml/week (50 ml, three times a week) during the last two weeks of the experiment. Additionally, the plants were given 50 ml of a 1 g/L Universol® Green low-phosphate fertiliser solution (N:P:K = 4:1:2) before watering during weeks 4 and 7, in order to ensure that nutrient availability in the pots was not a limiting factor for plant growth.

2.2.3 Data collection

A variety of physiological parameters were measured for all plants, so as to assess their competitive abilities in both climate scenarios. Throughout the duration of the experiment, height (cm) was recorded on a weekly basis for all plants. Also, photosynthetic measurements were taken during the last week of the experiment for the central *I. glandulifera* individuals in CI and I pots. Net photosynthesis (A), dark respiration (dr), transpiration (E) and stomatal conductance (gs) were analysed using a LI-6400 Infra-Red Gas Analyzer (IRGA, Licor, Lincoln, Nebraska, USA). All of these measurements were taken during ‘day time’ in the growth chambers, with values for dark respiration being obtained by covering the light sensors of the IRGA and the analysed leaf with an opaque cloth. Each measurement was taken three times, approximately 10 seconds apart, using the youngest fully-expanded leaves of central *I. glandulifera* plants in all cases.

After 9 weeks of growth, the aboveground biomass of all plants was harvested. Belowground biomass could only be separated and washed for CI pots, due to the previously stated involvement of C and I pots in a future experiment. All photosynthesising leaves were scanned and their areas were determined using the image processing program imageJ.

Furthermore, two root fragments were cut from each *I. glandulifera* plant in the CI pots and subsequently stained with a 0.035% Neutral Red dye, citric acid and NaOH solution. These fragments were also scanned while floating in a tray filled with water and their lengths were determined using the image analysis system winRHIZO. All plant biomass was then placed in a drying oven at 40°C for 48 hours and weighed once completely dry. Using these measurements I calculated the aboveground biomass and specific leaf area (SLA) of all plants, the specific root length (SRL) and stem mass fraction (SMF) of *I. glandulifera* individuals in CI pots, as well as the total and proportional biomass, leaf mass fraction (LMF) and root mass fraction (RMF) of all plants in CI pots. SMF could only be measured for *I. glandulifera* because it was the only species with a discernable stem.

2.2.4 Data analysis

The main focus of the analysis was on the effects of temperature on *I. glandulifera* - and, where possible, on native species - within the different communities, especially CI pots where the plants were grown in competition. Direct comparisons between the performances of invasive and native plants within one treatment were not likely to be revealing, as *I. glandulifera* is an annual plant, while all three native species are perennial and employ different growth strategies: *I. glandulifera* grew rapidly in order to be able to reproduce before dying at the end of the growth season, while the native species, grown from seed, reached considerably smaller sizes in the 8 weeks of the experiment. Thus, any direct differences in absolute height and biomass between natives and *I. glandulifera* could have been attributed to this life history strategy. Consequently, results regarding plant growth presented in this paper are predominantly focused on relative changes in height (growth rate) and biomass (proportion of invader and natives in a pot, rather than absolute mass). Also meaningful were the comparisons between plants from the same species growing under the two different temperatures, which can still offer insight into the effects climate change could have on physiological plant traits and the competitive abilities they determine.

All data except the photosynthetic measurements were transformed prior to analysis, in order to reduce SLA, SRL and biomass data skewness and permit the use of parametric tests (West, 2021). Height, absolute biomass, SLA and SRL data were log-transformed, while proportional biomass (i. e. the proportion of the total biomass produced in a pot represented by a certain species), SMF, RMF and LMF data were logit-transformed. All analyses were conducted in R, version 3.6.1 (R Core Team, 2019). Firstly, biomass, SLA and SLR analyses were carried out using a series of paired t-tests, as for each pot in the present climate chamber there was a plant belonging to the same seed family in the future chamber, grown in soil originating from the same sample. SLA analyses were conducted on all plants, but SLR tests were restricted to *I. glandulifera* in CI pots. Biomass analyses were mainly focused on CI pots where the harvest of the entire plant mass was possible. Sample size was in most cases 10 pairs, but along the duration of the experiment a C pot *J. vulgaris* and a CI pot *E hirsutum* individual died, so the relevant pair was eliminated completely (n = 9).

Secondly, I used linear mixed models ('lme4' R package; Bates *et al.*, 2015) to analyse height and photosynthetic measurement data. For the analysis of *I. glandulifera*, I used mean values for the three repeated measurement of net photosynthesis, dark respiration, transpiration and stomatal conductance. Mean values were used instead of a single measurement in order to achieve the highest level of accuracy possible, as values recorded for the four variables tended to change over short periods of time from the moment the IRGA chamber was placed on the leaf, making it difficult to choose the most correct timing for taking a measurement. Within the mixed model, temperature (present vs. future) was considered the fixed effect, while random variation at the individual plant level was taken into account as a random effect, due to the use of genetically similar pairs of plants in the two climate chambers. Height was analysed for all plants, using a model with climate, time and their interaction as fixed effects and random variation at plant level as a random effect once again. Model parameters in both instances were estimated by restricted maximum likelihood (REML).

2.3 RESULTS

2.3.1 Height

Increased temperatures stimulated growth in all plants, but had a stronger effect on natives than *I. glandulifera*. All species, regardless of the type of community from which they originated, tended to grow taller and their growth rates increased in the warmer climate of the future chamber (Table 2.2, Figure 2.3). The interaction term between time and climate was significant in all linear mixed models except for the one describing the growth of *E. hirsutum* in CI pots ($\beta = 0.0044$, SE = 0.0028, t = 1.584, $P = 0.116$; Figure 2.3C). *I. glandulifera* reached a greater final height than *E. hirsutum, J. vulgaris* and *S. dioica* in both the present (16.07 cm on average, compared to 2.22, 1.26 and 4.98 cm, respectively) and the future climate (20.52 on average, compared to 2.81, 2.05 and 6.28 cm, respectively). However, it displayed slower growth rates than native species in both chambers (Appendix 1; Figure 2.3), and warming had a weaker effect on invader growth (Table 2.2). Regardless of climate effects or community of origin, *J. vulgaris* had the steepest growth slopes, followed by *S. dioica* and *E. hirsutum* (Appendix 1; Figure 2.3). Similar trends were found in terms of the effects of higher temperatures on growth, with the exception of *E. hirsutum* in CI pots (Table 2.2).

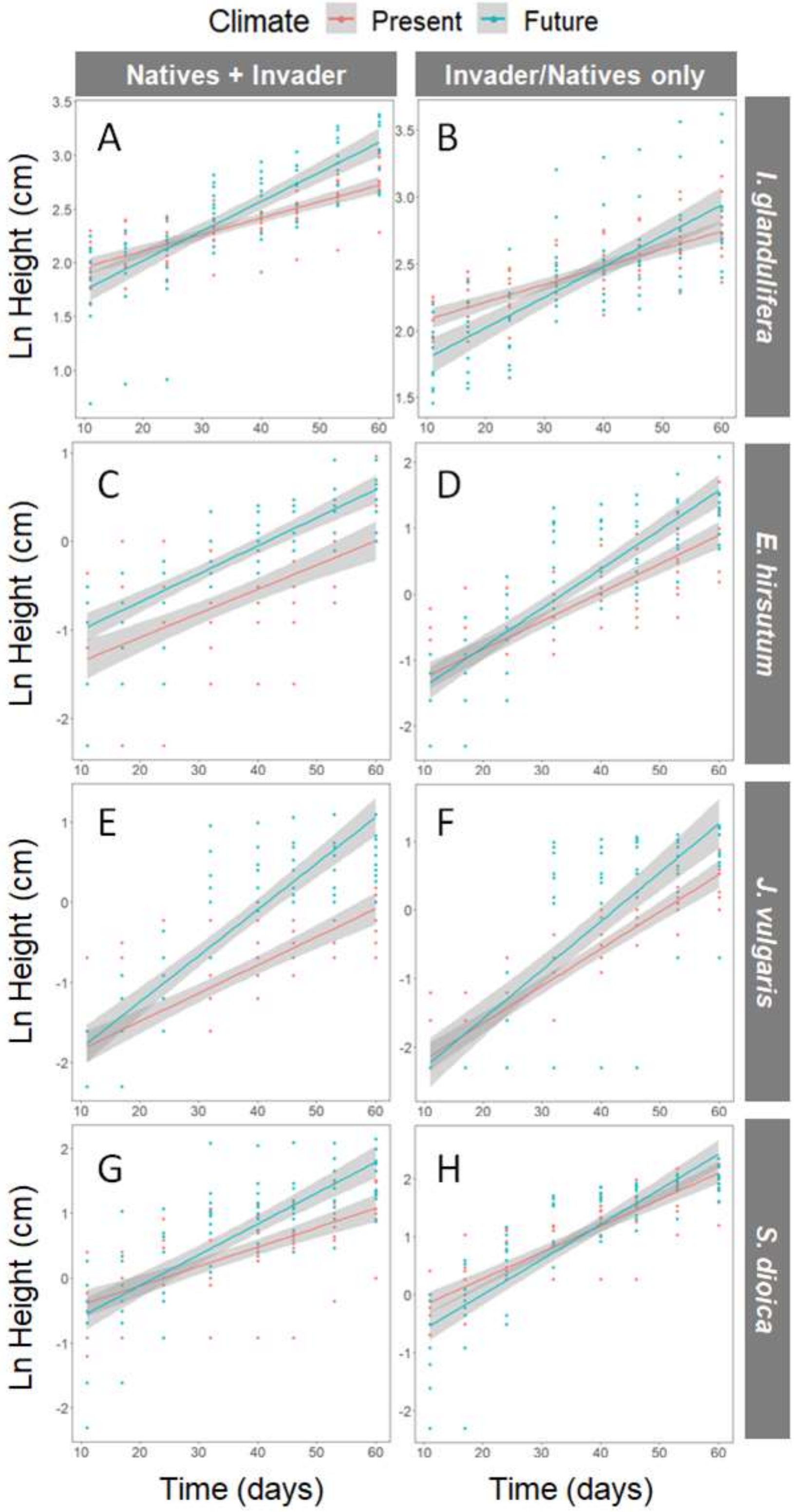

Figure 2.3. Comparison between changes in plant height (natural log transformed) over 60 days under current UK climate conditions (Present) and conditions reflecting a 3°C temperature increase (Future) for the invasive plant *I. glandulifera* (A-B) and three co-occurring native species (C-H). Plants were grown in communities comprising all four plants (A, C, E, G) or consisting of exclusively the invasive species (B) or the 3 natives (D, F, H).

Table 2.2. Summary statistics for linear mixed models describing the growth rate of the invasive plant *I. glandulifera* and three native species in two different climate conditions (current UK temperatures vs. 3°C warmer), grown either together or in communities exclusively comprising the invader or the natives; data were natural log-transformed.

Species	**Community Type**	**Climate x Time effect size**	**SE**	**df**	**t**	***P***
I. glandulifera	Natives + invader	0.012	0.001	138	9.361	<0.001
E. hirsutum	Natives + invader	0.004	0.003	124	1.584	0.116
J. vulgaris	Natives + invader	0.023	0.005	138	5.034	<0.001
S. dioica	Natives + invader	0.018	0.003	138	5.271	<0.001
I. glandulifera	Invader only	0.010	0.001	138	8.384	<0.001
E.hirsutum	Natives only	0.016	0.004	138	4.501	<0.001
J. vulgaris	Natives only	0.017	0.006	124	2.905	0.004
S. dioica	Natives only	0.015	0.004	138	3.366	<0.001

2.3.2 Biomass accumulation and allocation

Although the plants grew taller and had accelerated growth rates, they did not tend to accumulate more biomass aboveground. Warming did not have a significant effect on the dry aboveground biomass of CI (paired t-test, t = -1.799, df = 9, *P* = 0.106) or C pots (t = 1.268, df = 9, *P* = 0.237), but it did increase the overall aboveground biomass measured in I pots (t = 2.933, df = 9, *P* = 0.017). However, this biomass gain could not be attributed to the target central *I. glandulifera* individual, as its aboveground biomass did not differ significantly between the two climates (t = 0.457, df = 9, *P* = 0.659). None of the individual species in C pots were affected by the climate treatment in terms of biomass (*E. hirsutum*: t = -1.238, df = 9, *P* = 0.247; *J. vulgaris*: t = -0.894, df = 8, *P* = 0.397; *S. dioica*: t = 1.337, df = 9, *P* = 0.214). When grown together with the invader, the aboveground biomass of *J. vulgaris* (t = 3.176, df = 9, *P* = 0.011) and, marginally, *S. dioica* (t = 2.403, df = 9, *P* = 0.04) increased in the warmer climate, while *I. glandulifera* (t = 0.812, df = 9, *P* = 0.438) and *E. hirsutum* (t = -0.824, df = 8, *P* = 0.434) did not experience any significant change in absolute aboveground biomass.

Despite the fact that warming did not seem to affect plant communities overall in terms of productivity, it appears that it had an effect on the competition between *I. glandulifera* and its native neighbours. Total (aboveground and belowground) plant biomass in CI pots was not significantly different between the two chambers (t = 2.011, df = 9, *P* = 0.075), but the proportion of *I. glandulifera* was lower in the future chamber, dropping on average by 8.31% (t = -2.691, df = 9, *P* = 0.025; Figure 2.4) in the warmer climate. Evidence suggests that the majority of this loss in invader biomass occurred at the root level, *I. glandulifera* exhibiting a mean decrease in proportional belowground biomass of 15.49% (t = -4.124, df = 9, *P* = 0.003; Figure 2.4). In contrast, the native species which displayed the greatest growth, *S.*

dioica, showed a significant increase in proportional biomass overall of 5.72% (t = -2.489, df = 9, *P* = 0.035), as well as belowground of 9.12% (t = 3.709, df = 9, *P* = 0.005; Figure 2.4). No significant effect of climate was detected on the aboveground proportion of either *I. glandulifera* (t = -1.616, df = 9, *P* = 0.141) or *S. dioica* (t = 1.637, df = 9, *P* = 0.136). These results indicate that increased temperatures might have promoted the suppression of invader root growth by native species. I only mention here the results relevant to the two species because they made up the majority of the biomass measured in CI pots, *E. hirsutum* and *J. vulgaris* making only a small contribution to total biomass (6.79% in the present chamber and 9.38% in the future chamber).

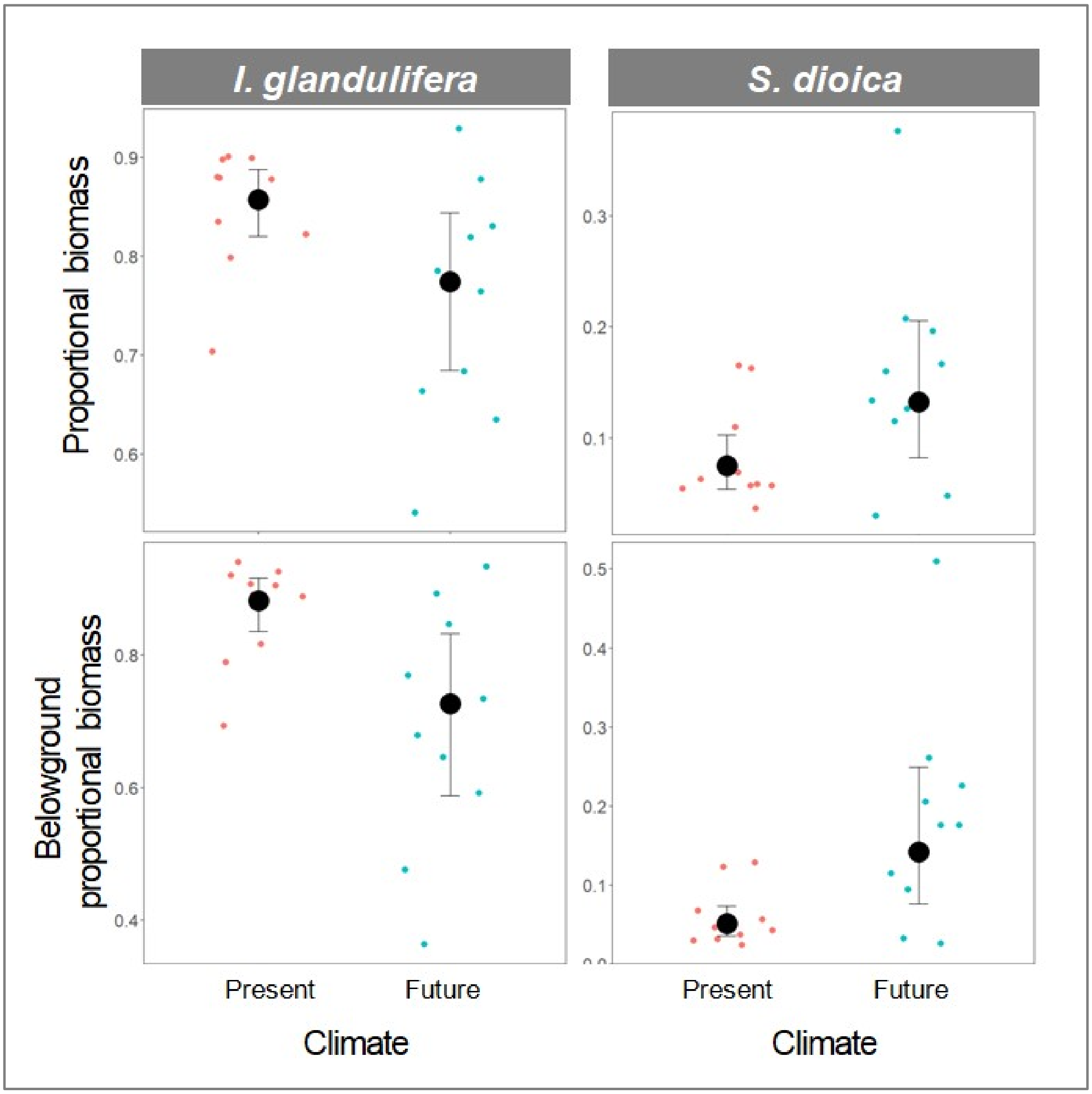

Figure 2.4. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on total and belowground proportional biomass of the invasive species *I. glandulifera* and a co-occurring native species, *S. dioica* after 9 weeks of growth. Means and standard errors illustrated here were obtained through the back-transformation of logit-transformed data. Coloured data points show the distribution of the raw proportional data.

Biomass allocation patterns were changed by higher temperatures only in the invader and one of the native species. Warming did not have a significant effect on the RMF or LMF of either *E. hirsutum* (RMF: t = -1.638, df = 8, *P* = 0.140; LMF: t = -0.513, df = 8, *P* = 0.622) or *J. vulgaris* (RMF: t = 1.398, df = 9, *P* = 0.196; LMF: t = -1.092, df = 9, *P* = 0.303). The effect of climate on *I. glandulifera* RMF was also marginally non-significant, despite an observable decrease (t = -2.113, df = 9, *P* = 0.064; Figure 2.5). However, *I. glandulifera* experienced a 3.48% decrease in LMF (t = -2.381, df = 9, *P* = 0.041; Figure 2.5) and a 7.8% increase in

SMF (t = 3.846, df = 9, *P* = 0.004; Figure 2.6) in the warmer climate of the future chamber. Finally, higher temperatures had the greatest effect on *S. dioica* individuals, which invested 12.63% more in roots (t = 4.522, df = 9, *P* = 0.001; Figure 2.5) and 9.15% less in leaves (t = -2.698, df = 9, *P* = 0.025; Figure 2.5) in the future chamber.

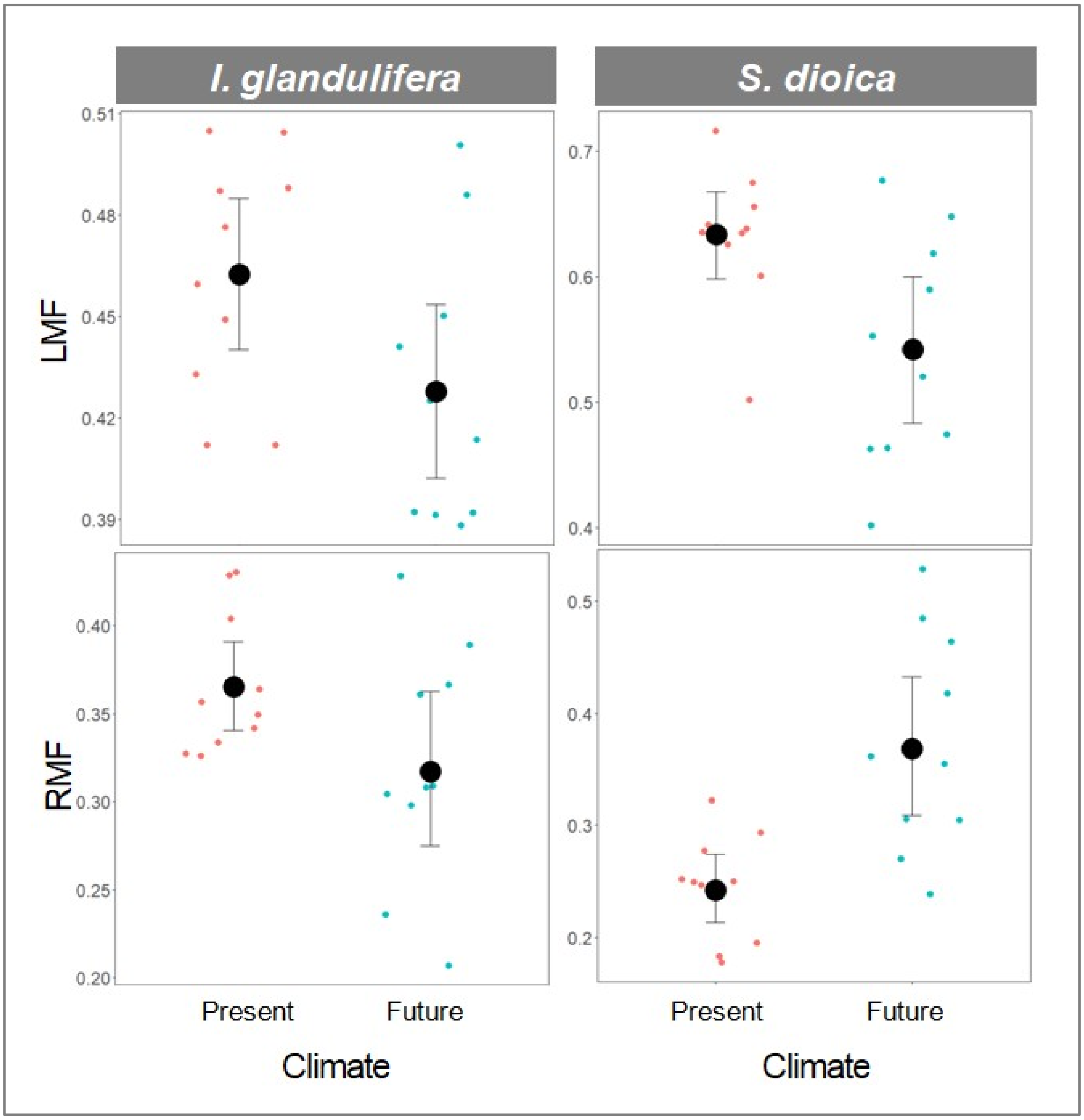

Figure 2.5. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on the root mass fraction (RMF) and leaf mass fraction (LMF) of the invasive species *I. glandulifera* and a co-occurring native species, *S. dioica* after 9 weeks of growth. Means and standard errors illustrated here were obtained through the back-transformation of logit-transformed data. Coloured data points show the distribution of the raw proportional data.

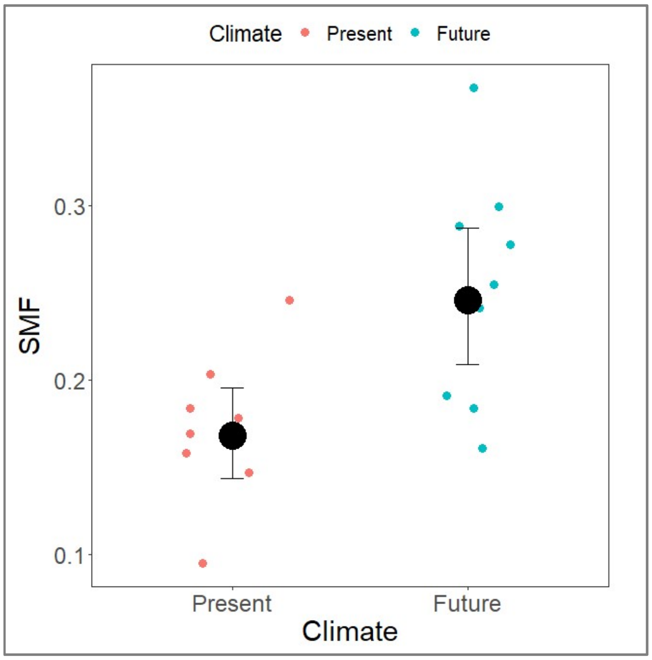

Figure 2.6. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on the stem mass fraction (SMF) of the invasive plant species *I. glandulifera* after 9 weeks of growth. Means and standard errors illustrated here were obtained through the back-transformation of logit-transformed data. Coloured data points show the distribution of the raw proportional data.

2.3.3 Leaf and root economics

I. glandulifera only exhibited changes in SLA when grown in competition with natives. There was no significant difference between the two climates in SLA for *I. glandulifera* individuals grown with conspecifics (t = 1.380, df = 9, *P* = 0.201; Figure 2.7), but climate did have a positive impact on *I. glandulifera* SLA in CI pots (t = 2.393, df = 9, *P* = 0.040; Figure 2.7). Native species responded differently to the change in climate. There was no evidence to suggest warming had any effect on SLA on *J. vulgaris* and *E. hirsutum*, in either CI pots (*E. hirsutum*: t = 1.087, df = 8, *P* = 0.309; *J. vulgaris*: t = 1.817, df = 9, *P* = 0.103) or C pots (*E. hirsutum*: t = -0.164, df = 9, *P* = 0.873; *J. vulgaris*: t = 1.821, df = 8, *P* = 0.106). However, *S. dioica* showed a significant increase in SLA, regardless of pot of origin (CI: t = 3.446, df = 9, *P* = 0.007; t = 3.518, df = 9, *P* = 0.007; Figure 2.7). Lastly, in terms of SRL in *I. glandulifera* from CI pots, no significant effect of climate was detected (t = -1.411, df = 8, *P* = 0.196; Figure 2.8).

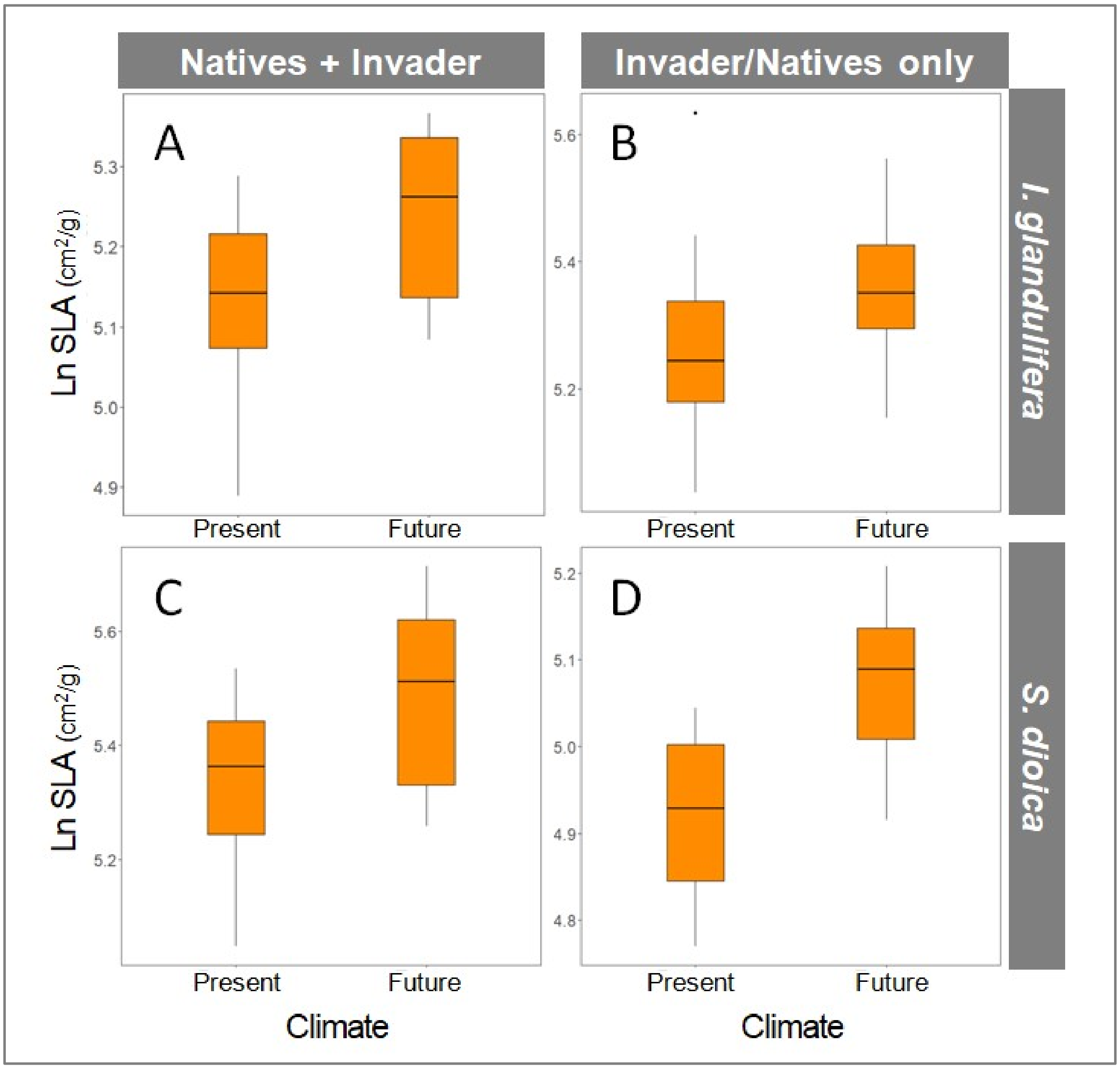

Figure 2.7. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on medians and interquartile ranges for the specific leaf area (log-transformed) of the invasive species *I. glandulifera* (A-B) and a co-occurring native species, *S. dioica* (C-D). Plants were grown for 9 weeks in communities comprising *I. glandulifera* and three native species, including *S. dioica* (A, C) or consisting of exclusively the invasive species (B) or the 3 natives (D).

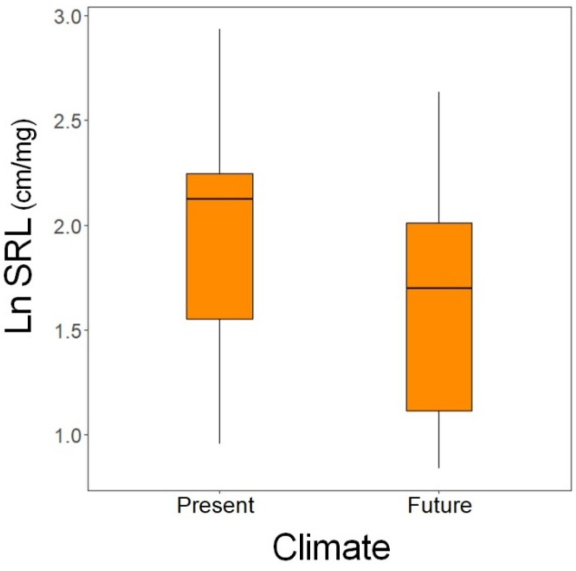

Figure 2.8. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on medians and interquartile ranges for the specific root length (log transformed) of the invasive species *I. glandulifera* after 9 weeks of growth.

The models did not reveal any significant effects of higher temperatures on net photosynthesis, dark respiration or transpiration rates of *I. glandulifera*, regardless of the type of community the plants originated from (Table 2.3, Figure 2.9). However, stomatal conductance rates significantly decreased in both CI pots (β = -0.0930, SE = 0.0328, t = -2.834, *P* = 0.011; Figure 2.9D) and I pots (β = -0.0630, SE = 0.029, t = -2.125, *P* = 0.048; Figure 2.9D).

Table 2.3. Summary statistics for linear mixed models analysing photosynthetic parameters in the invasive plant *I. glandulifera* in two different climate conditions (current UK temperatures vs. 3°C warmer); models were fitted separately for *I. glandulifera* grown together with three native species and individuals grown with other conspecifics for 9 weeks.

Trait	Community Type	Climate effect size	SE	df	t	*P*
Net photosynthesis	Natives + invader	-0.368	0.389	18	-0.946	0.357
	Invader only	-0.068	0.414	18	-0.163	0.872
Dark respiration	Natives + invader	0.042	0.253	18	0.164	0.871
	Invader only	0.172	0.166	18	1.039	0.313
Transpiration	Natives + invader	-0.275	0.152	18	-1.814	0.086
	Invader only	0.026	0.182	18	0.145	0.887
Stomatal conductance	Natives + invader	-0.093	0.033	18	-2.834	0.011
	Invader only	-0.063	0.030	18	-2.125	0.048

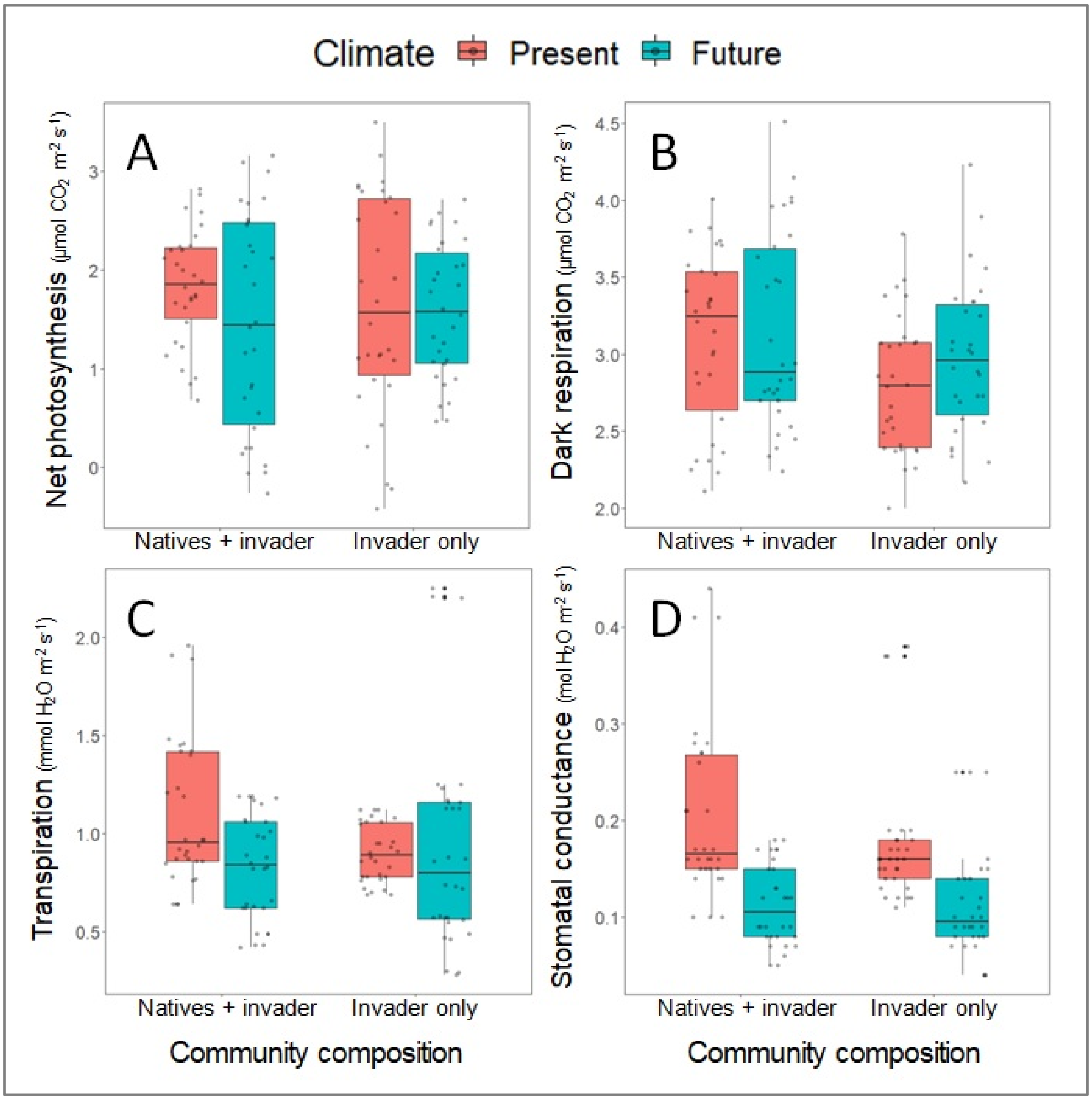

Figure 2.9. Effects of climate warming (Present – reflects current UK conditions; Future - 3°C warmer) on medians and interquartile ranges for the (A) net photosynthesis (B) dark respiration (C) transpiration (D) stomatal conductance rates of the invasive species *I. glandulifera*, grown either with native species or with conspecifics for 9 weeks.

2.4 DISCUSSION

The results of this experiment show that higher temperatures can impact the competitive abilities of both invasive and native plants through changes in performance-related physiological traits. For *I. glandulifera* plants, the effects of climate were positive for some of these traits, but negative for others, highlighting the trade-offs invaders must manage when competing with native communities in a changing climate. Warming increased *I glandulifera* height and, thus, its ability to compete for light, but it did so not by accumulating more biomass, but by allocating greater resources to lengthening stems, to the detriment of its leaves and roots. While it seemed to compensate for decreased leaf investment by increasing specific leaf area (i. e. maximising leaf area given a certain leaf mass) when grown in competition with natives, photosynthetic processes in *I. glandulifera* leaves were not affected by climate, with the exception of a decrease in stomatal conductance in the warmer climate. These effects led to a significant drop in the total invader proportion within the pot, mainly due to a drop in the belowground proportional biomass component of the invader. These changes might have allowed *S. dioica* to better compete for limiting nutrients in the pots where all plants were present.

Effects of climate were stronger for the native species, but impacted all three in different ways. For *J. vulgaris* and *E. hirsutum*, climate effects were only identified in terms of growth rates, which were substantially increased by warming, with the exception of *E. hirsutum* from combined pots. Even so, *J. vulgaris* and *E. hirsutum* individuals grew significantly less than both *I. glandulifera* and *S. dioica*, especially in pots where all species were grown together, and they did not show any changes in leaf or root functional traits. *S. dioica*, on the other hand, was the strongest native competitor of *I. glandulifera* and the results suggests that it could owe this success to an ability to respond to the changing climate through alterations in biomass allocation patterns and leaf economics. Similar to the invader, *S. dioica* also allocated less biomass to leaves in the warmer climate and attempted to compensate for this by increasing its specific leaf area, but investment in the root system increased considerably, which accounts for the difference in belowground invader biomass. These adjustments could have allowed *S. dioica* to better compete for limiting resources within the pot and grow considerably more than the other native species. Thus, some native species could be able to become better competitors against invasive plants and possibly limit their spread under climate change.

For certain physiological traits, *I. glandulifera* and the natives responded in similar ways. Despite rates of height increase being stimulated by warmer temperatures for nearly all plants used in this study, aboveground biomass did not significantly change in neither pots where all plants were grown together, pots exclusively containing natives, nor the target *I. glandulifera* in invader only pots. The only notable changes were the increased aboveground biomasses of *S. dioica* and *J. vulgaris* as a response to warming when in competition with the invader. However, the effect of climate on growth was stronger for native species than for *I. glandulifera*, especially when they were growing under competition with the invader. This finding is consistent with those of other studies which showed that natives, particularly in riparian zones where the species used here originate from, are habitat specialists which are more likely to be affected by changes in environmental conditions than more generalist invaders (Verlinden and Nijs, 2010; Flanagan *et al.*, 2015; also, see Chapter 1). On the other hand, in the case of one native species, *E. hirsutum*, competition with *I. glandulifera* seemed to override the impact of warming and hinder growth, which supports the idea that invasions are extremely context-dependent and that particular attention needs to be paid to species-specific responses to competition.

Another cause of the greater effect of temperature on natives might be the high variability of *I. glandulifera* height data, as the invasive species reached considerably greater and more variable heights than the natives. This variation could be attributed to possible etiolation (i.e. the development of weak stems with long internodes, as a result of insufficient light availability), as suggested by the fact that dark respiration rates were consistently higher than net photosynthesis, meaning that light intensity in the growth chambers was not fully saturating for photosynthesis. However, visual inspections at the time of the experiment did not provide evidence of etiolation, as there were no visible differences in internode lengths between the growth chamber plants and plants from wild populations observed in the field, as well as *I. glandulifera* plants investigated by my colleague in the soil moisture experiment. Regardless, the two growth chambers had the same light intensity settings, so comparisons between effects of the two temperature treatments on *I. glandulifera* can still be confidently drawn.

I. glandulifera and *S. dioica* also responded in similar ways to the increased temperature, through increasing specific leaf area values. Higher SLA values have been associated with a shorter leaf life-span, as well as enhanced photosynthesis and dark respiration rates and, thus, a greater capacity for rapid growth (Reich *et* al., 1992; Leishman *et al.*, 2009). However, an increase in SLA, characterised by thinner leaves, can lead to poorer water conservation abilities, as water can more rapidly diffuse through the leaf and be eliminated (McDowell, 2002; Van den Boogaard and Villar, 1998). Decreased water use efficiency might prove to be problematic for plants growing in higher temperatures, where evapotranspiration is increased. It is possible, then, that *I. glandulifera* leaves had decreased stomatal conductance rates in the warmer climate in order to prevent water loss. *I. glandulifera* only had significantly increased SLA values when competing with natives though, which might point towards an added stress on plants which are invading native communities and competing with indigenous species rather than growing in monocultural stands. Furthermore, heating did not enhance the invader's photosynthetic rate by the end of the experiment, which is in contrast with findings from other studies (Gianoli and Molina-Montenegro, 2021), indicating that *I. glandulifera* did not invest a great deal of resources in compensating for the loss in leaf biomass caused by the higher temperature, possibly because light intensity in the growth chambers was not saturating for photosynthesis. In contrast, *S. dioica* exhibited higher SLA even when in the uninvaded pots, indicating that it was also a strong competitor against the other native species. There is a possibility, then, that the invasibility of a riparian plant community might be determined not by the entire assemblage, but by the presence of some highly competitive and dominant native species. A similar conclusion about the importance of native competitor identity was put forward by Power and Sanchez Vilas (2020), who observed that in an artificial community, comprised of four native species invaded by *I. glandulifera*, only the *Urtica dioica* limited the invader's growth.

Higher temperatures also seemed to promote the competitive root growth suppression of *I. glandulifera* by *S. dioica*. In addition to reduced leaf investment under warming, *I. glandulifera* individuals did not experience any changes in tested root functional traits: root mass fraction and specific root length. Such biomass allocation responses to heating, where the plant invests in rapid shoot growth rather than root growth, is seen in other invasive species as well (Wang *et al*., 2011). Similarly, a meta-analysis by Wu *et al.* (2011) using data from warming experiments executed in various ecosystems found that generally warming seems to affect aboveground biomass more strongly than belowground or total biomass. However, *S. dioica* allocated more resources to root growth, which lead to significant increases in the proportion of native biomass in the pots. A reason why *S. dioica* displayed changes which contrast with these patterns might be that the meta-analysis focused on plants from terrestrial habitats, while the natives used in the present experiment were riparian species. Belowground responses may be of greater importance to the latter, as they might be less tolerant to heat-induced drought in these habitats where water is normally a readily available resource.

Investment in root system development could also more be beneficial to a perennial native such as *S. dioica* in preparation for upcoming growth seasons, as opposed to *I. glandulifera* where each individual experiences only one growth season. However, in wild populations, priority effects could influence competitive outcomes in ways that are not reflected in a pot experiment involving perennial plants grown from seed. In the present experiment the invader made up the majority of biomass produced in a pot, but other studies have shown that well-established perennial natives can out-compete annual invasive species, even under a range of nutrient availability scenarios (McGlone *et al.*, 2012) and even if in the first year of the perennial's growth annual invaders showed better competitive abilities (Corbin and D'Antonia, 2004). Long-term performances between a mix of annual and perennial invasive and native species need to be compared and investigated in future climate experiments spanning multiple years, in order to achieve a greater understanding of the ways in which the dynamics of these types of plants might be impacted by climate change.

The results of this study suggest that, despite *I. glandulifera* growth being stimulated by climate warming, the plant's competitive abilities might decrease, due to trade-offs between different traits related to invasiveness in relation to environmental constraints. The species seems to be more plastic aboveground than belowground, as more rapid lengthening is achieved by investing more biomass in stems, rather than leaves and roots. The considerably greater plant heights observed in *I. glandulifera* compared to natives might aid the plants in achieving greater light reception and, thus, may be an important competitive advantage. However, the fact that flower buds at harvest were only found on plants grown in a warmer climate indicates growth seasons might shorten due to faster growth. These findings are in accordance with the body of evidence present in the literature according to which phenological changes might be a common response of invasive plants to climate change (Wolkovich *et al*., 2013). As a consequence, *I. glandulifera* growth seasons might shorten to such an extent that they will die earlier in the season and not shade natives for as long as they are currently doing. *I. glandulifera* individuals dying earlier might also not succeed in producing as many seeds as usual. Thus, higher temperatures could decrease the invasiveness of *I. glandulifera* promote the success of co-occurring natives in the future, which is a hypothesis worth exploring in future research.

Although my results point towards a reduction in invasion success of *I. glandulifera* under future warming, these inferences should be made with caution, as other interacting factors must be considered. It is important to note here that direct comparisons between plants originating from different types of communities could not be drawn with a high degree of accuracy, as any observed differences could be attributed to the different number of individuals in each type of community: CI pots contained 4 plants each, while I and C pots only contained 3, due to pragmatic experimental design considerations. Thus, the importance of native-invader competition could have been misinterpreted, as reduced growth in natives in CI pots, compared to C pots, might also be related to space and nutrient limitations due to the greater number of plants present in the pot. However, the apparent effects of higher temperatures on individual community types, as previously discussed in this section, can still convey valuable information about the future of the competition between invasive and native riparian plants under climate change, albeit in a less direct manner.

In wild populations, other factors could also play a major role in determining invasion success for exotic riparian plants. For example, invasive plant responses to climate change might be affected by other types of global change, such as the anthropogenic degradation and fragmentation of habitats (Marini *et al*., 2011). As areas heavily modified by humans are often associated with an abundance of invasive species, due to intense disturbance regimes, high resource supply and high rate of plant introductions, continued human activity already seems to be facilitating plant invasions, regardless of any new climatic limitations the plants might experience under future climate change (Hulme, 2009). Furthermore, riparian invasive plants' spread could still dependent on the intensity of human-mediated spread of invasive propagules within uninvaded habitats, in addition to passive propagule transport provided by the river system (Bellini and Becker, 2021). For example, studies investigating invasive plant distribution along elevation gradients or across landscapes have concluded that lower invasive plant density at certain sites can more often be attributed to lower human presence and intervention, rather than to climate constraints (Pysek *et al.,* 1998; Willis and Hulme, 2002; Ross *et al.,* 2008). Finally, the plants in the chamber simulating future climate were heated constantly throughout the experiment, but recent papers suggest that separate day and night warming can have differential effects on the competition between invasive and native plants, due to changes in carbon sequestration. Su *et al.* (2021) found that night warming favoured invasive species by improving their competitive suppression of native plant root growth, but day warming increased the net photosynthetic rate of natives, while decreasing it for invasives. Asymmetrical changes in temperature could, thus, have unexpected consequences for plant invasion dynamics in the field.

In conclusion, increased temperatures caused by global change could directly impact the physiology and life-history traits of invasive and native plants and, thus, competition outcomes for invaded plant communities. Consequently, climate-induced changes might lead to a future decrease in the success of *I. glandulifera* in riparian habitats, depending on how well native species are able to cope with increased temperatures as well and provide biotic resistance to invasion. The evidence gathered here also suggests that the identity of the native species could be important in predicting the community's susceptibility to invasion. Moreover, perennial and annual species are likely to adopt very different strategies in response to higher temperatures, which might prove to be useful in designing management strategies. However, besides the direct effects identified in this study, changes in physiological traits can also have indirect implications for management (Lu *et al.,* 2013; Lu *et al.,* 2014; Prince *et al.*, 2018). Consequently, it is essential to understand the species-specific interactions between plant physiology, climate and competitive success, in order to improve invasive species management planning in the context of an increasingly warmer and more unstable climate.

CHAPTER 3

How will climate-induced changes in soil moisture affect the competitive abilities of the riparian invasive species *Heracleum mantegazzianum?*

3.1 INTRODUCTION

Increasing global temperatures due to ongoing anthropogenic greenhouse gas emissions are associated with major modifications in precipitation patterns worldwide (IPCC, 2014). As a consequence, it has been predicted that future climate change could have great effects on the dynamics of river systems by drastically increasing or decreasing water tables, as well as altering flowing regimes and sediment deposition patterns (Serrat-Capdevila *et al*., 2007; Vansteenkiste *et al*., 2012). Findings from modelling approaches suggest that riverbank vegetation will be severely impacted by these climate-induced changes in flow regimes and seasonal hydrology (Rood *et al*., 2008; Rivaes *et al*., 2014). On one hand, some changes could directly lower riparian plant survivorship. For example, diminished river flows in summer, when plants' water requirements are highest due to evapotranspiration, can lead to drought stress and even increased mortality (Rood *et al*., 2008). On the other hand, changes in the natural flow regimes, to which riparian plant life history traits are connected, might have an influence on processes of seedling recruitment and plant succession (Rivaes *et al*., 2014). It is possible, for instance, that in future conditions desynchronisation might occur between plant physiological traits, like seed release timing, and aspects of river hydrology, such as the spring peaks in water flow necessary for seedling establishment (Rood *et al*., 2008).

Modified riparian plant assemblages and increased variability in environmental and hydrological conditions could provide opportunities for non-native species to become established by taking advantage of new unexploited niches in riparian ecosystems, which are already considered to be highly susceptible to plant invasions (Naiman and Decamps, 1997; Tickner *et al*., 2001). Furthermore, the spread of previously established invasive species could be promoted if the survival, growth and performance of native plants decrease, rendering them less able to compete with invaders under the new environmental conditions and resource availability scenarios (Sorte *et al*., 2013). However, whether hydrological alterations will be hindering or aiding plant invasions is still unclear on a case-by-case basis, which adds uncertainty to management planning, as some strategies could become ineffective in some areas, while restoration opportunities could arise in others (Bradley *et al*., 2010). Thus, it is imperative for ecologists to gain a deep understanding of how these two major forms of global change are interacting, and will continue to interact, within riparian zones.

As global temperatures increase, climatic models predict an intensification of the hydrological cycle leading to more abundant precipitation in some areas (Bloschl *et al.*, 2019), a considerable decrease in other areas, especially arid or semi-arid habitats (Seager *et al.*, 2007; Serrat-Capdevila *et al.*, 2007; Bloschl *et al.*, 2019), as well as a general trend toward increased variability and seasonality (Katz and Brown, 1992; Frei *et al.*, 2006). Riparian habitats are also likely to be greatly exposed to more extreme climatic events resulting in intense floods and droughts (Senior *et al.,* 2002; Capon *et al.*, 2013). However, many studies investigating the potential effects of climate change on river hydrology and riparian vegetation focus on waterflow as a form of disturbance (Truscott *et al.*, 2006; Stromberg *et al.*, 2007). Less attention has been paid to water as a resource and soil moisture as a potential influencing factor in riparian invasion dynamics.

Fluctuations in resource availability are a critical factor in determining the level of susceptibility to invasion of a certain habitat and subsequent invasion success (Davis *et al.*, 2001). Resource pulses could decrease the pressure to compete with co-occurring species and allow non-native plants to establish, while deficits in limiting resources can lead to more intense competition, making invasion outcomes more dependent on the competitive abilities of both invasive and native plants (Stohlgren *et al.*, 1999; Davis *et al.*, 2001). In experiments, this concept is usually linked to nutrient availability alone or in concert with water availability (Maron and Marler, 2008; Zhang *et al.*, 2016), but the relationship between riparian plant invasions and changing precipitation patterns can be difficult to discern from the plethora of interacting factors. Nevertheless, important effects of soil moisture levels on invasive plant establishment patterns have been identified in other types of habitats, such as grasslands and prairies, as well as drylands such as the ones in southeastern US (Goergen and Daehler, 2002; Miller *et al.*, 2006; Blumenthal *et al.*, 2008). Considering the abundance of ecosystem functions and services provided by riparian habitats, as well as their disproportionately large biodiversity compared to other habitat types (Naiman and Decamps, 1997; Capon *et al.*, 2013), it is worth investigating whether the same effects can be observed in vegetation on river banks.

Experimental manipulations have hitherto revealed varied outcomes for the interaction between invader success and water availability. It has repeatedly been put forward that invasive plants are more resistant to both increases and declines in water tables than noninvasive species grown in the same conditions (Kercher and Zedler, 2004; Wang *et al.*, 2015). This resistance has sometimes been attributed to certain physiological traits such as height and specific leaf area, as well as a high degree of plasticity in the expression of these traits (Conti *et al.*, 2017). For example, plant height and biomass are considered to be essential in maintaining the structural integrity of plants in the face of fluctuating water quantities, as well as allowing them to better compete for other resources simultaneously, such as sunlight (Hamilton *et al.*, 2005). Moreover, lower specific leaf areas are associated with more efficient strategies of resource uptake, which decreases a plant's need to compete with the other plants around it and makes it more resilient in the face of resource variability (Goldberg and Landa, 1991; Conti *et al.*, 2017). Higher SLA values can lead to poorer water conservation abilities, as water can more rapidly diffuse through the thinner leaves and be eliminated (McDowell, 2002; Van den Boogaard and Villar, 1998).

Physiological and life-history traits of both invasive and native plants, as well as the competitive abilities derived from them, can mediate their responses to fluctuations in soil moisture. Water excess has been shown to favour wetland invasive species rather than co-occurring natives through altered carbon and nitrogen plant-soil cycles and enhanced rates of nutrient release and uptake from litter (Wang *et al.*, 2015; Wang *et al.*, 2018). On the other hand, non-native riparian species seem to display greater establishment rates and water conservation abilities once established than co-occurring natives under drought conditions (Vandersande *et al.*, 2001, Perry *et al.*, 2012). Similarly, the literature indicates that a variety of non-native riparian and wetland plant species exhibit greater growth in environments characterised by more variable water tables and soil moisture (Miller and Zedler, 2003). However, other studies have reported contrasting results, where water additions either favoured natives or inhibited invasive plant growth (Vandersande *et al.*, 2001; Zhang *et al.*, 2016), or it did not affect competition between invasive and native plants (Lempe *et al.,* 2008; Maron and Marler, 2008). Therefore, effects seem to be species and context-specific and similar experiments need to be carried out on a wider variety of riparian invasive plant species.

Heracleum mantegazzianum Sommier & Levier (Giant Hogweed; Gilman, 2015) is a highly successful invasive plant in Europe and the British Isles, with considerable impacts on indigenous vegetation structure and function, as well as human health due to its phototoxic properties (Pysek *et al.*, 2007; Thiele and Otte, 2007; Chan *et al.*, 2011; Jandova *et al.*, 2014). Invasion success for this species has been linked to access to river corridors and could, thus, be impacted by climate-driven changes in soil moisture (Thiele and Otte, 2007). Through the present experiment, I assessed the ways in which plant height and biomass (a frequently used parameter for measuring the level of invasion in a plant community; van Kleunen *et al.*, 2010) in both *H. mantegazzianum* and four co-occurring native riparian species is impacted by a variety of watering regimes reflecting predicted changes in precipitation quantity and variability. I also investigated whether any changed in *H. mantegazzianum* growth were reflected in changes in specific leaf area. An important objective of this study is to investigate whether variations in soil moisture have differential effects on the invasiveness of *H. mantegazzianum* and the invasibility of the native community. This aim was achieved by particularly focusing on biomass production and discussing whether the invader's biomass itself is affected by the watering treatments (invasiveness), or whether just the proportion of invasive plant biomass within the community changes, regardless of the absolute growth of *H. mantegazzianum* (invasibility). These mechanisms underpinning observed effects of environmental variables on biological invasions are not often rigorously separated in discussions of similar studies, but it is important to do so in order to gain greater insight into invasion dynamics in a changing climate.

3.2 METHODS

3.2.1 Study species and seed preparation

The focus of this experiment was on an important perennial invader in Central European river catchments: *Heracleum mantegazzianum* Sommier & Levier (family Apiaceae). Local native communities were simulated using four co-occurring vascular plant species native to County Durham: *Epilobium hirsutum* L.(Gilman, 2015), *Rumex obtusifolius* L (Gilman, 2015), *Chamaenerion angustifolium* L. (Komiljon *et al.*, 2020), and *Centaurea nigra* L. (Mirek *et al.*, 2020). These species, all perennials, were selected because they were readily available and they germinate easily. Wild populations found in and around Durham City, County Durham, along the river Wear, were used to obtain seeds for *H. mantegazzianum* (54.7764 N, 1.5687 W; 54.7731 N, 1.5728 W; 54.7814 N, 1.5738 W), *E. hirsutum* (54.7764 N, 1.5675 W), *R. obtusifolius* (54.7711 N, 1.5593 W), *C. angustifolium* (54.7737 N, 1.5542 W) and *C. nigra* (54.7711 N, 1.5593 W). A variety of locations were chosen for the collection of *H. mantegazzianum* seeds in order to obtain a range of genotypes and maximise the chances of germination. Prior to the experiment, *H. mantegazzianum* seeds were subjected to cold stratification in tubes filled with wet sand at 4°C for 4 months, in order to break dormancy. During this period, the seeds germinated and the seedlings were transplanted to the experimental pots directly from the tubes. Seeds from native species were sown on moist sand and allowed to germinate and grown for 4 weeks (February to March 2021) in a greenhouse setting (21°C, ambient lighting) before transplanting.

3.2.2 Experimental set-up and watering treatments

The experiment was carried out inside a greenhouse at Durham University's Botanic Garden over a 10-week period (March 24th to June 2nd, 2021), coinciding with the plants' natural growth season. A colleague's identical parallel experiment using the invasive plant *I. glandulifera* instead of *H. mantegazzianum* was also executed, 70 plant pots being allocated to each experiment. Thus, a total of 140 pots, each with a 20 cm diameter and 3 L capacity, were filled with J Arthur Bower's Top Soil and then randomly arranged in the greenhouse (Figure 3.1A). Within the greenhouse, plants were grown in ambient conditions, in accordance to natural conditions for the specified time of year. In order to account for differences in these conditions, such as light availability, pots were randomised once more at the end of week 5. *H. mantegazzianum* seedlings grown from seeds collected from 10 different plants (siblings) were transplanted into the middle of each pot, while seedlings from the four native species were planted in the surrounding corners (Figure 3.1B). Where possible, I used seedlings showing at least one pair of true leaves (i.e. excluding cotyledons).

Figure 3.1. Experimental set-up: layout of pots in the greenhouse (A) and an example experimental community, with the invasive species in the middle, surrounded by native plants (B)

10 pots were assigned to each of the 7 watering treatments, every pot within a lot of 10 containing a *H. mantegazzianum* seedling belonging to a different set of sibling seeds, so as to reduce confounding effects related to genetic variation. The plants were watered three times a week according to the volume of water required for each of the 7 treatments. Pots subjected to the first 3 treatments were watered with a constant amount of water throughout the experiment: 300 ml for every water dose given in the constant high treatment, 150 ml for constant medium and 50 ml for constant low (Figure 3.2, 1-3). Treatments 4 and 5 were started after 5 weeks of growth and consisted in a single water pulse and a water deficit, respectively (Figure 3.2, 4-5). Plants were initially watered with a medium amount of water (150 ml three times a week), which was replaced by either 300 ml or 150 ml, accordingly, for the following 3 weeks. Finally, the last two treatments involved a 3 week pulse and a 3 week deficit in succession, with the pulse coming first in treatment 6 and the deficit in treatment 7 (Figure 3.2, 6-7). These treatments started after 2 weeks of growth in medium watering conditions and ended after 6 weeks. The exact water quantities used for the treatments were initially chosen somewhat arbitrarily and intuitively, but with the goal of achieving a full range of soil moisture conditions, reflective of a spectrum spanning from drought to water-logged. I later evaluated whether this objective was reached through analyses of variation in soil moisture between the seven treatments (see Results).

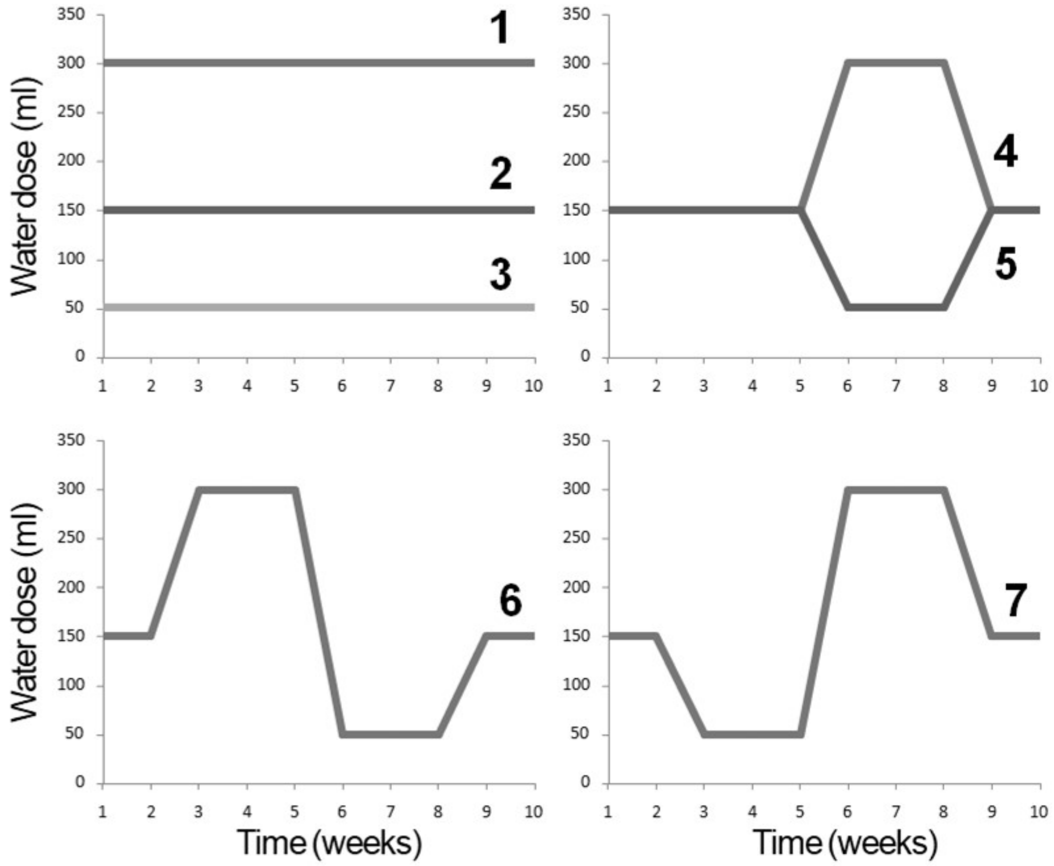

Figure 3.2. Watering treatments used on communities consisting of the invasive plant *H. mantegazzianum* and four co-occurring native species: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

3.2.3 Data collection

Only two parameters were monitored throughout the duration of the experiment, as most of the data were collected at the end of week 10. Firstly, in order to determine whether the intended treatments were successfully reflected in reality, soil moisture was measured at three different points during the experiment (weeks 2, 5 and 10) using a HH2 Moisture Meter (Theta Probe, Delta T devices, Cambridge, UK). Secondly, stem height were measured every 2 weeks, starting from week 5, after the plants were well established. After 10 weeks of growth, the aboveground biomass of all plants was harvested, alongside the belowground biomass from 5 pots out of each treatment lot. Photosynthesising *H. mantegazzianum* leaves were scanned and their areas were determined using the image processing program imageJ. These areas were utilised in calculating specific leaf area (SLA) for *H. mantegazzianum* under the different watering treatments. All plant biomass was placed in a drying oven for 48 hours, at 40°C and weighed once completely dry.

3.2.4 Data analysis

Data were transformed prior to analysis as follows: SLA, height and absolute biomass data were natural log-transformed, while logit-transformations were applied to proportional *H. mantegazzianum* biomass (proportion of biomass produced within a pot represented by *H. mantegazzianum*) and volumetric water content data obtained using the soil moisture meter. ANOVAs and post-hoc Tukey's tests were used in order to investigate differences in the aforementioned variables between the 7 watering treatments. The focus was placed on more relevant groupings of the treatments. Firstly, all other treatments were compared to the "baseline" constant medium treatment. Secondly, the single pulse treatment was compared to both the constant high treatment and treatment 7, where the pulse was preceded by a deficit. All three of these treatments involved watering the plants with the highest amount of water in the latter half of the experiment. Thus, I investigated whether the effects of a "flooding" event later in the growing season would vary depending on whether the event was preceded by either drought conditions (treatment 7), another flooding event (treatment 3) or a medium amount of water (treatment 4). Equivalent comparisons were drawn between treatments 1 (constant low), 5 (one deficit event) and 6 (pulse-deficit), where it is drought that occurs later in the growing season.

These comparisons were drawn in order to gain insight into the significance for plant growth of both short (treatments 4 and 5) and longer-term (treatments 1 and 3) flooding and drought events in isolation, as well as in association with other extreme events (treatments 6 and 7), as an increase in the frequency and unpredictability of such events has been put forward as a possible consequence of climate change in river systems. Finally, the pulse-deficit and deficit-pulse treatments were contrasted, so as to assess the importance of the timing and order of such events on *H. mantegazzianum* performance, since changes in seasonal flow regimes and their associated peaks and lows, to which plants are currently adapted, are also predicted to occur under climate change. All analyses were conducted in R, version 3.6.1 (R Core Team, 2019).

3.3 RESULTS

3.3.1 Soil moisture

The results of the soil moisture analysis indicate that water quantities were chosen correctly for representing a gradient of conditions, from drought to water-logging. Soil moisture appeared to be higher in week 5, at the halfway-point of the experiment for all treatments, except for treatments 3 and 7, which are the only treatments where the plants were subject to a water deficit in the first half of the experiment (Figure 3.3). Soil moisture was then lower at the end of the experiment, possibly due to naturally higher June temperatures and sunlight quantities outside the greenhouse. Nevertheless, ANOVA tests showed there were overall significant differences in resulting soil moisture between the 7 watering treatments at all time points, as was intended: week 2 (F = 16.98, df = 6, $P < 0.001$), week 5 (F = 74.91, df = 6, $P < 0.001$), and week 10 (F = 44.12, df = 6, $P < 0.001$). Post-hoc Tukey tests revealed that under treatment 1 (constant high) soil moisture was higher at all time points than under treatment 2, constant medium (Appendix 2; Figure 3.3A). Similarly, the soil was consistently drier under treatment 3 (constant low) than treatment 2 (Appendix 2; Figure 3.3A).

As expected, there were no differences in soil moisture between treatment 4 (one pulse) and treatment 2 in the first 5 weeks, as treatment 4 was only applied from week 5 until week 8 (Appendix 2; Figure 3.3B). Furthermore, by the end of week 10 when the next measurement was taken, soil moisture in treatment 4 pots was once again not significantly different from the medium treatment (Appendix 2; Figure 3.3B). Similar results were obtained for treatment 5 (water deficit between weeks 5 and 8), as no significant differences were detected during weeks 5 and 10. However, at the beginning of the experiment, in week 2, soil moisture was lower in treatment 5 pots than constant medium treatment pots (Appendix 2; Figure 3.3B). Finally, treatments 6 (water pulse before week 5, then deficit until week 8) and 7 (water deficit until week 5, then pulse until week 8), initially showed respective differences in resulting soil moisture (higher for treatment 6, lower for treatment 7) compared to treatment 2 during weeks 2 and 5, but were again similar to the constant medium treatment at the end of week 10 (Appendix 2; Figure 3.3C).

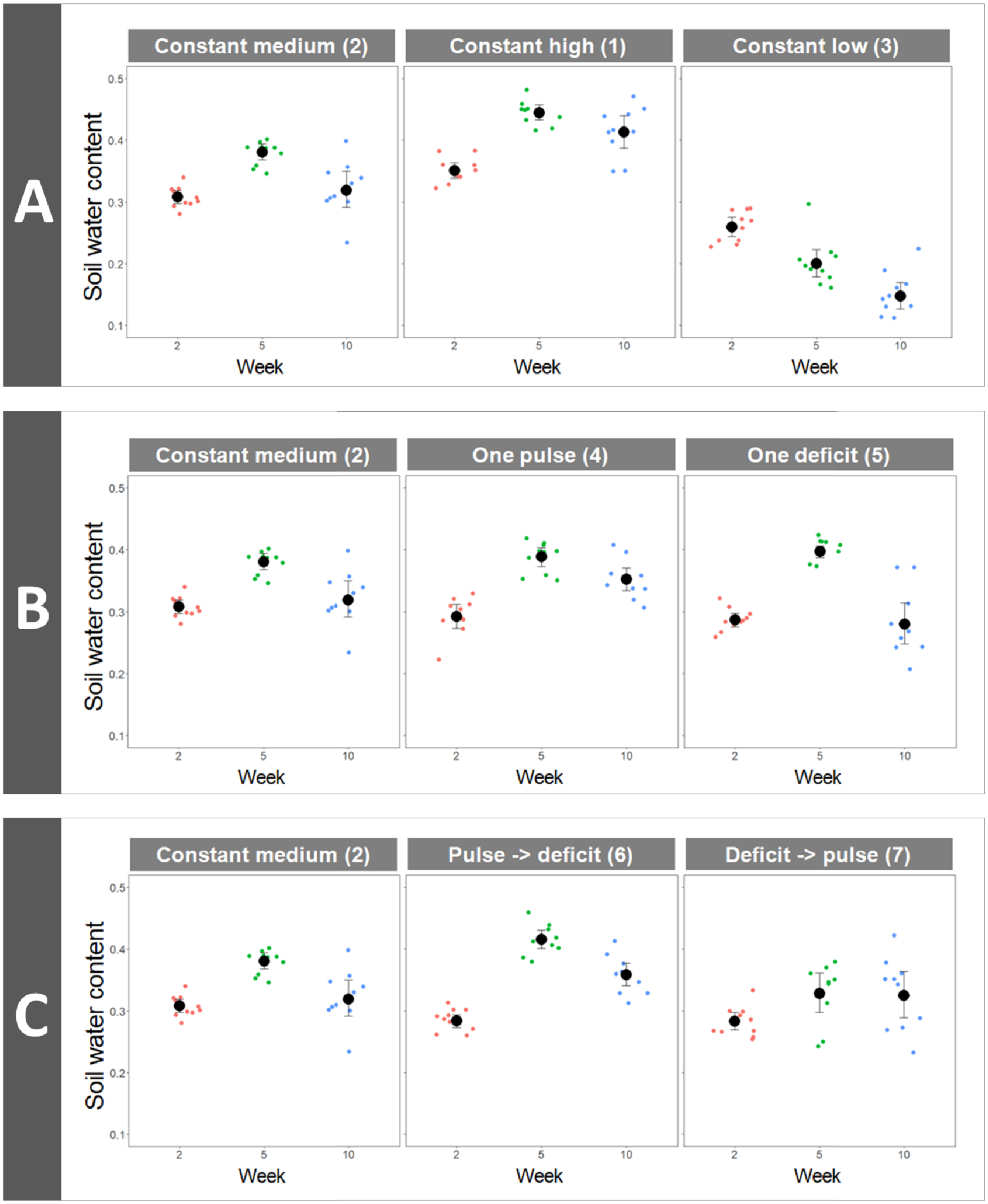

Figure 3.3. Comparisons of soil water content (proportion) between the baseline watering regime (treatment 2) and the other 6 treatments, at three different time points: prior to the commencement of treatment 6 and 7 in week 2, at the halfway point of the experiment when treatments 4 and 5 started, and at the end of the experiment, in week 10. Means and standard errors illustrated here were obtained through the back-transformation of logit-transformed data. Coloured data points show the distribution of the raw proportional data.

3.3.2 Height

Significant differences in plant heights between treatments were observed much later for *H. mantegazzianum* than for native species. *H. mantegazzianum* heights were not significantly affected by any of the treatments until week 5, at the midpoint of the experiment (ANOVA, F = 0.95, df = 6, *P* = 0.46; Figure 3.4). By week 8, however, differences in heights were observed (ANOVA, F = 3.48, df = 6, *P* = 0.005; Figure 3.4; Table 3.1), with plants watered with a consistently high volume of water being shorter than both the plants from the constant medium and single pulse treatments (Figure 3.4; Table 3.1; Appendix 4). Similarly, plants growing in a constant water deficit were shorter than the ones from the medium and single drought event treatments (Figure 3.4; Table 3.1; Appendix 4). These effects were consistent until the end of the experiment (ANOVA, F = 4.46, df = 6, *P* = 0.001; Table 3.1), but by week 10 the individuals which had been subjected to water deficit for 3 weeks were taller than the plants which had also been subjected to a water pulse prior to the deficit (Figure 3.4; Table 3.1; Appendix 4). No other effects of the 7 treatments on *H. mantegazzianum* heights were detected (Table 3.1; Appendix 4).

The 7 watering regimes had similar effects on the four native species (Appendix 3) and, thus, I will be describing these effects here only in relation to the best growing species, *R. obtusifolius*, as it is representative for the entire native community and allows for greater clarity in illustrating the results. In the case of natives, differences in heights between plants from different treatments could be observed at all time points (Appendix 3). *R. obtusifolius* heights were affected by the same treatments and in the same direction as *H. mantegazzianum* heights, but throughout the experiment (ANOVA, week 5: F = 16.39, df = 6, *P* < 0.001; week 8: F = 26.50, df = 6, *P* < 0.001; week 10: F = 21.80, df = 6, *P* < 0.001; Table 3.1, Appendix 4). In addition to those contrasts, plants that had been subjected to a water pulse event, followed by a deficit event were also shorter than plants watered with a medium amount of water and the plants which were subjected to this treatment in the reverse order (Table 3.1, Appendix 4).

Table 3.1. Significant pairwise comparisons (ANOVA test, followed by post-hoc Tukey's test) between the effects of 7 watering treatments on plant height for *H. mantegazzianum* and the best-growing native competitor, *R. obtusifolius*. Green indicates a significant difference ($P < 0.05$). Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

Species	**Week**	**Pair**										
		1-2	**3-2**	**4-2**	**5-2**	**6-2**	**7-2**	**1-4**	**7-4**	**3-5**	**6-5**	**7-6**
H. mantegazzianum	5											
	8	🟩	🟩					🟩		🟩		
	10	🟩	🟩					🟩		🟩	🟩	
R. obtusifolius	5	🟩	🟩			🟩		🟩		🟩	🟩	🟩
	8	🟩	🟩			🟩		🟩		🟩	🟩	🟩
	10	🟩	🟩			🟩		🟩		🟩	🟩	🟩

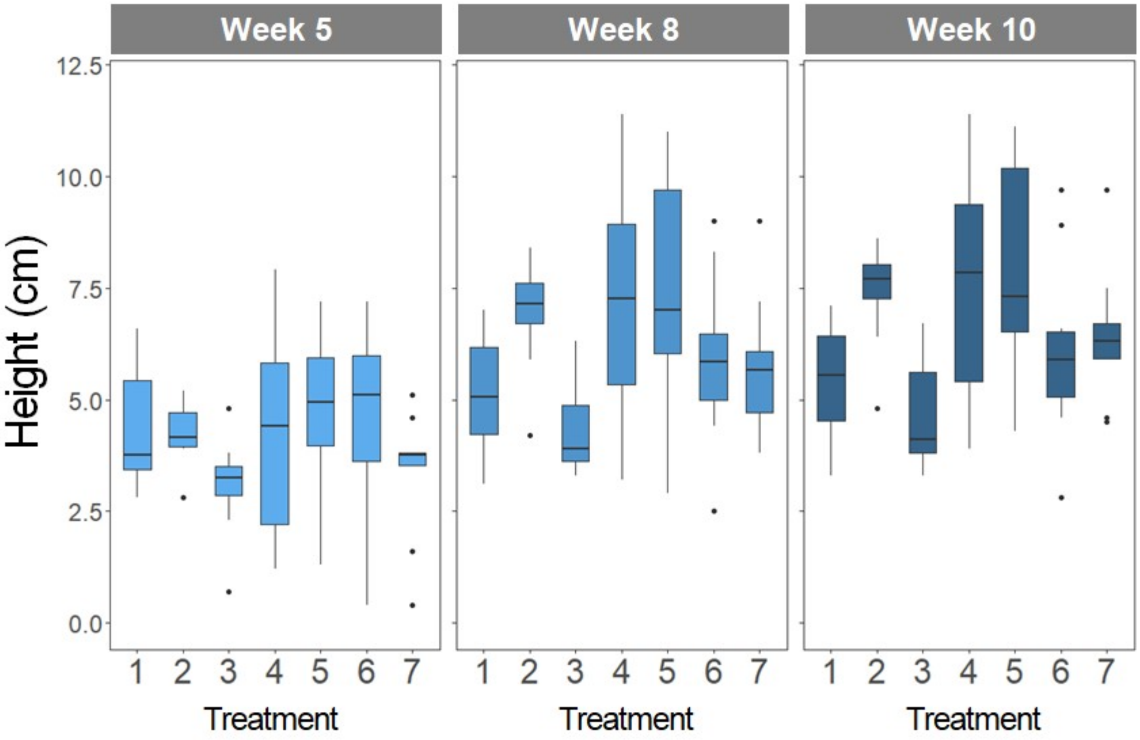

Figure 3.4. Effect of 7 different watering treatments on medians and interquartile ranges for the height (cm) at 3 different time points of *H. mantegazzianum* grown with four native species. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

3.3.3 Biomass

As predicted by the wide range of studies on water availability effects on plant performance, total plant biomass produced in the pots was considerably impacted by the watering treatments applied (ANOVA, F = 13.73, df = 6, *P* < 0.001). The least productive communities were those which had received a constant high quantity of water and those within the pulse, followed by deficit treatment (Figure 3.5A). Pots subjected to constant drought also produced less biomass than the pots that were optimally watered and the ones that had only experienced one drought event (Table 3.1, Appendix 5). Biomass within the one pulse, one deficit and deficit, followed by pulse treatments did not differ significantly from the baseline (Table 3.2, Appendix 5). All of these effects were also consistent when dividing plant mass into aboveground biomass (ANOVA, F = 21.98, df = 6, *P* < 0.001) and belowground biomass (ANOVA, F = 11.94, df = 6, *P* < 0.001). Additionally, aboveground biomass was greater in the pots where the water pulse was preceded by a deficit event than those which had only received the pulse (Table 3.2, Appendix 5).

H. mantegazzianum biomass was not significantly impacted by watering regimes (ANOVA, F = 1.15, df = 6, *P* = 0.36; Figure 3.5C), not even when considering the aboveground (ANOVA, F = 0.72, df = 6, *P* = 0.63) and belowground components separately (ANOVA, F = 2.81, df = 6, *P* = 0.03, but only one pairwise comparison was significant and it was not of interest) . However, soil moisture impacted the proportion of *H. mantegazzianum* in the community overall (ANOVA, F = 11.67, df = 6, *P* < 0.001), as well as the aboveground (ANOVA, F = 10.34, df = 6, *P* < 0.001) and belowground biomass (ANOVA, F = 13.75, df = 6, *P* < 0.001). I discovered opposite trends between community biomass and *H. mantegazzianum* proportion. The highest proportions of *H. mantegazzianum* were measured in the pots with the lowest biomass production, i.e. the pots that were subjected to the constant high (50% invader on average) and pulse followed by deficit treatments (22% invader on average; Figure 3.5).

However, under the constant deficit treatment, both community biomass and *H. mantegazzianum* proportion were low (Figure 3.5) and no significant differences were detected between this treatment and the one drought event treatment (Table 3.2, Appendix 5). Results pertaining to invader proportion under treatment 7 (deficit, followed by pulse) also deviate from the aforementioned trend. While treatment 7 only had an effect on community aboveground biomass in comparison to the single pulse treatment, it decreased both aboveground and belowground *H. mantegazzianum* proportional biomass (Table 3.2, Appendix 5). Furthermore, it lowered invader proportion by 4% overall and 6% at root level compared to the baseline treatment (Table 3.2, Appendix 5). Invader proportion in pots where the constant deficit, one pulse and one deficit treatments were applied did not differ significantly from the constant medium treatment (Table 3.2, Appendix 5).

Table 3.2. Significant pairwise comparisons (ANOVA test, followed by post-hoc Tukey's test) between the effects of 7 watering treatments, applied for 10 weeks to a community consisting of *H. mantegazzianum* and four native species, on total community biomass and absolute and proportional biomass of *H. mantegazzianum*. Green indicates a significant difference ($P < 0.05$). Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

Variable	**Mass type**	**Pair**										
		1-2	**3-2**	**4-2**	**5-2**	**6-2**	**7-2**	**1-4**	**7-4**	**3-5**	**6-5**	**7-6**
Total plant biomass	Total	🟩	🟩			🟩		🟩		🟩	🟩	🟩
	Aboveground	🟩	🟩			🟩		🟩	🟩	🟩	🟩	🟩
	Belowground	🟩	🟩			🟩		🟩		🟩	🟩	🟩
***H. mantegazzianum* biomass**	Total											
	Aboveground											
	Belowground											
***H. mantegazzianum* proportion**	Total	🟩				🟩	🟩	🟩			🟩	🟩
	Aboveground	🟩				🟩		🟩	🟩		🟩	🟩
	Belowground	🟩				🟩	🟩	🟩	🟩		🟩	🟩

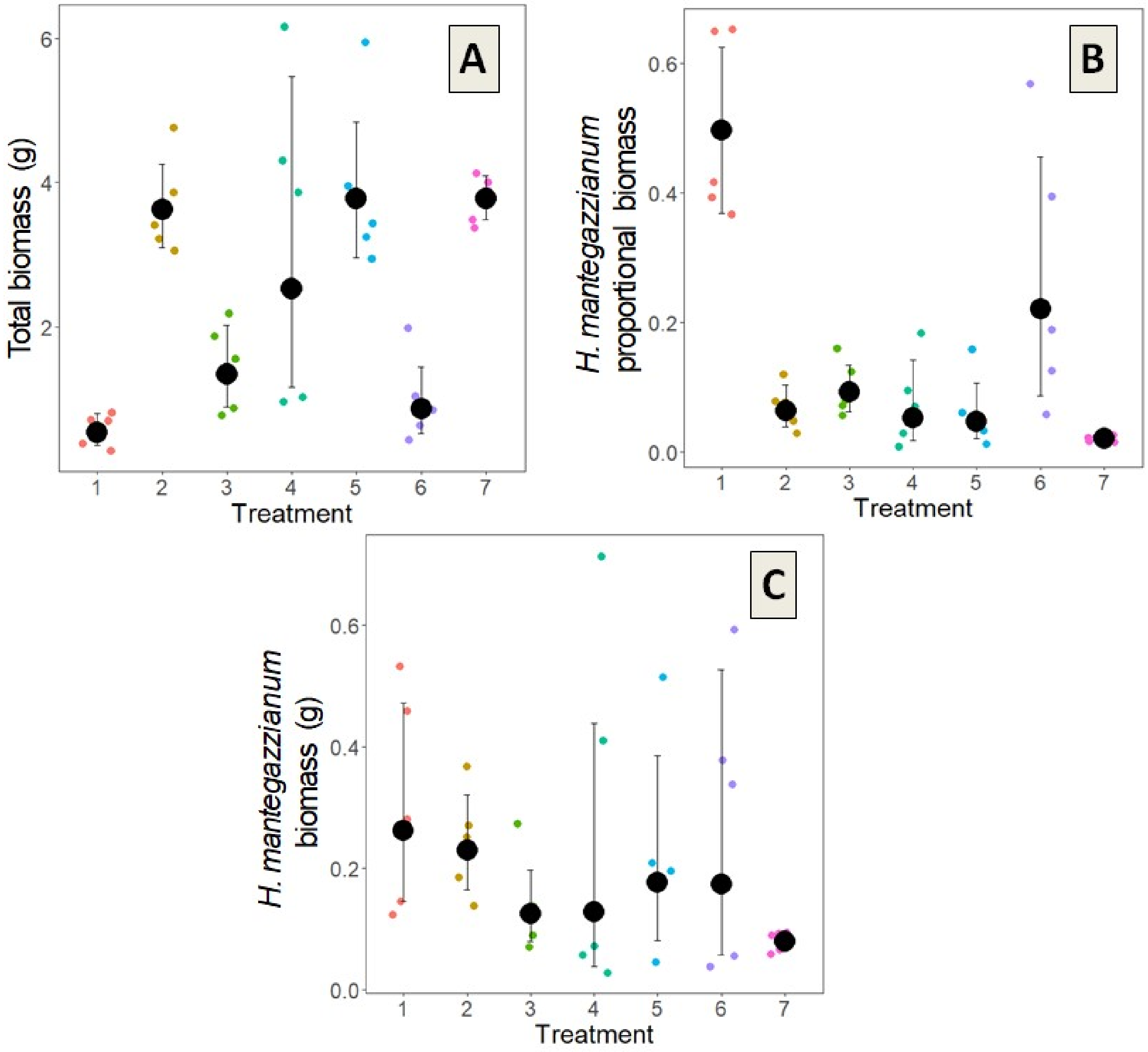

Figure 3.5. Effects of 7 different watering treatments, applied for 10 weeks to a community consisting of *H. mantegazzianum* and four native species, on: (A) total plant biomass (g); (B) *H. mantegazzianum* proportional biomass; (C) *H. mantegazzianum* absolute biomass (g). Means and standard errors illustrated here were obtained through the back-transformation of logit-transformed data. Coloured data points show the distribution of the raw proportional data. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

3.3.4 Specific leaf area (SLA)

The lack of variation in *H. mantegazzianum* biomass between treatments is consistent with the lack of variation in specific leaf area. No significant effects of soil moisture on SLA were detected in *H. mantegazzianum* leaves after 10 weeks of growth (ANOVA, F = 0.93, df = 6, *P* = 0.48). However, sample sizes between treatments were different, as in the constant deficit treatment only 5 plants with viable leaves remained at the end of the experiment.

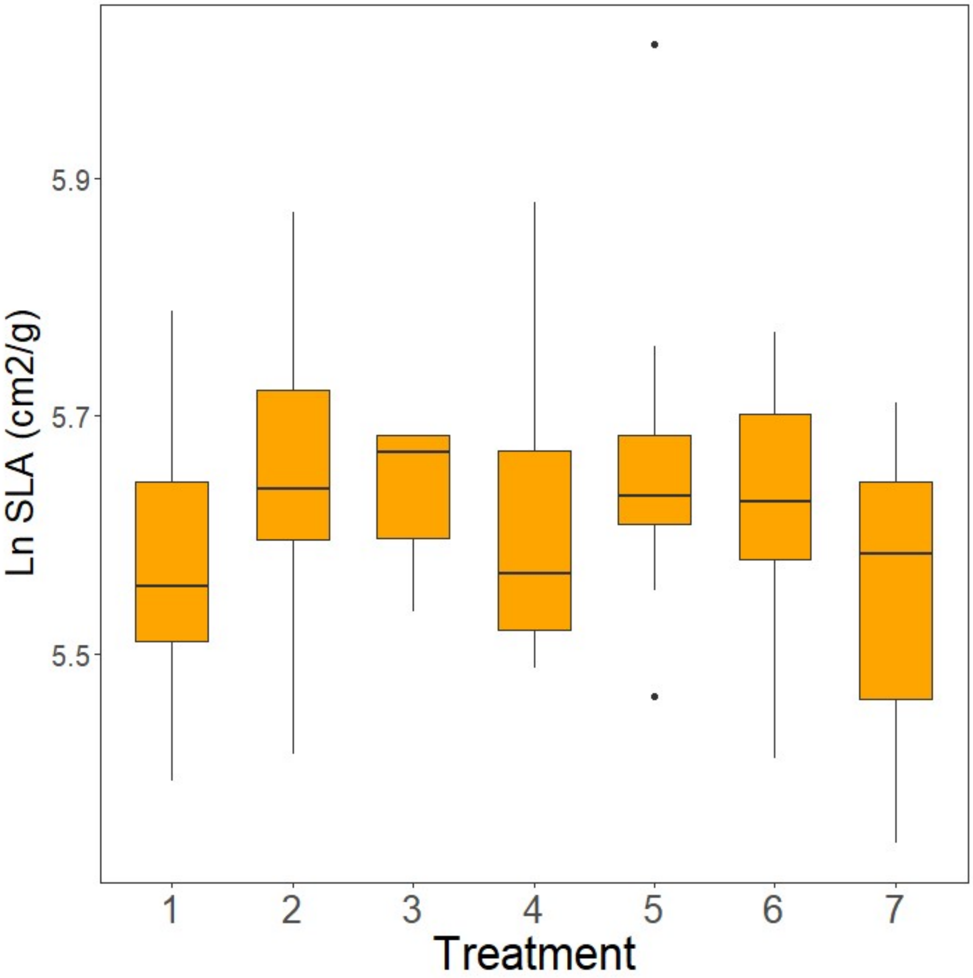

Figure 3.6. Effect of 7 different watering treatments on medians and interquartile ranges for the specific leaf area (log-transformed) of the invasive species *H. mantegazzianum* grown with four native species for 10 weeks. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse.

3.4 DISCUSSION

Overall, native species were more severely impacted by changes in soil moisture than *H. mantegazzianum*. Invader biomass production remained consistent across the 7 watering treatments both aboveground and at root level, and differences in plant heights between treatments were observed much later in the experiment than in the case of the native species. Native growth was greatly hindered by excessive watering early in the experiment, which allowed *H. mantegazzianum* to become the predominant plant in those communities due to its higher resilience and tolerance to these conditions. Consequently, it was apparent that these early soil moisture conditions did not stimulate fitness-related traits in the invasive species and, thus, its invasiveness, but rather increased the native community's vulnerability to invasion. However, although single drought events did not affect plant growth, both the invader and the native species were inhibited by prolonged drought, which not only impacted the performance and competitive abilities of the plants, but also their survival. Finally, when an excess of water was received in the second half of the experiment, growth was not negatively impacted and was even stimulated when the excess was preceded by a period of drought.

An increasing body of literature is attempting to shed light on whether flooding in riparian and wetland habitats promotes plant invasions and the particular mechanisms through which this occurs. In some species, excessive irrigation enhances the invasiveness of non-native plants. For example, in an observational experiment, the wetland invasive species *Phragmites australis* was favoured and grew better in areas with higher flooding levels, possibly due to its greater ability to accumulate carbon and conservatively use limiting nutrients in the context of flood-induced changes in soil nutrient ratios and availability (Wang *et al.*, 2015). In contrast, *H. mantegazzianum* coped better than natives with conditions which diminished native growth and exploited the increased invasibility of the community, without its growth being improved. Flooding tolerance could be thus an essential characteristic determining invasion success in riparian habitats in the future. However, some prolific non-native species do not seem to have superior physiological adaptations to increased water quantities. For instance, the wetland invasive *Lythrum salicaria* reacts physiologically in the same manner to flooding as its native congeners, by increasing plant height and forming specialised tissues at the base of the plant that regulate gas exchange between the plant and the atmosphere, even when partly submerged (Lempe *et al.*, 2008). Greater water availability might give the invader an initial advantage, but evidence shows that continued submergence eventually inhibits invader growth as well, as the submerged parts, especially the roots, are negatively impacted by the oxygen shortage that occurs (Zhang *et al.*, 2016). Moreover, robustness of native communities in the face of invasions when being experimentally irrigated has been demonstrated even in other, less diverse habitats, such as grasslands (Maron and Marler, 2007).

Ready access to water is often cited as an important reason for the proliferation of invasive plants along river corridors (Naiman and Decamps, 1997; Richardson *et al.*, 2007). Nevertheless, the responses of riparian invasive species to periods of water deficit are not well documented, but the presence of non-native competitors has been shown to further reduce plant-available soil water (Maron and Marler, 2008). Drought conditions and their negative impacts on plant growth are routinely linked with elevated salinity levels and there is evidence to suggest invasive plants might have greater water use efficiency in high salinity conditions (Vandersande *et al.*, 2001). However, in the present experiment, both *H. mantegazzianum* and its native competitors were equally inhibited by low soil moisture and the invader was not able to capitalise on the increase in community invasibility seen in some of the other treatments. Lowering SLA is a strategy employed by some plants in order to improve water conservation (McDowell, 2002), but I did not find any such changes in *H.*

mantegazzianum. Plants under severe drought stress usually close their stomata in order to cope, leading to reduced carbon assimilation rates, which might explain the stunted growth of all species involved (Jaiphong *et al.*, 2015). Studies on non-riparian species have discovered similar patterns of suppressed biotic resistance to invasion of the native community under drought stress, with the invasive species' growth also being inhibited in parallel (Har-Edom and Sternberg, 2010; Conti e*t al.*, 2017).

In this study, the succession order of high and low water events had a great influence on growth for the native community and, consequently, on its ability to resist invasion by *H. mantegazzianum*. When water was supplied in excess early in the growth period and was followed by a drought episode, native plants were considerably less productive, allowing the invader to thrive, but when the order was reversed, the opposite trend emerged. A possible explanation is that plants which were shortly subjected to drought conditions soon after being planted were forced to invest resources in establishing stronger root systems, which they subsequently used to take advantage of the sudden increase in resources and quickly recover in terms of growth. In similar experiments, an increase in CO_2 assimilation was observed upon re-irrigating (Jaiphong *et al.*, 2015). For native individuals which were exposed to higher than usual soil moisture early, investing in rapid root development might not have been a priority and they could not cope with the abrupt decrease in water availability later. This possible explanation for the observed relationship between the timing of drought/flood events and native growth could also be supported by the fact that root biomass followed the same trends as overall biomass when comparing plants under the two treatments. Variability in resources is often thought to promote biological invasions (Parepa *et al.*, 2013). Consequently, predicting the future of *H. mantegazzianum* invasions under increasingly variable precipitation patterns might pose some difficulty, as the order in which weather events occur during the growth season seem to be important to native vegetation and to its ability to compete against invasive species.

Although the present study highlights clear effects of soil moisture on the competition between *H. mantegazzianum* and co-occurring native species, the inferences that can be made from the results are limited by the short time frame of the experiment. As *H. mantegazzianum* is a monocarpic perennial plant, conducting similar experiments spanning multiple growing seasons could be extremely useful in understanding the possible impact of climate-induced changes in water availability on its competitive abilities. Changes in seasonal precipitation might also be important, as other species have shown differential responses to changes in summer and winter precipitation (Bradley *et al.*, 2010). For example, high winter precipitation increased invasions in a northwestern American prairie habitat, with little effects recorded for summer precipitation (Blumenthal *et al.*, 2008), while in a California grassland habitat, increased water supply promoted plant invasions when it was applied in spring, but not in winter (Thomsen *et al.*, 2005). Moreover, in natural populations, the relationship between invasive plants' germination rates and climate change have mostly been discussed in relation to temperature (Gillard *et al.*, 2017a; Gillard *et al.*, 2017b), but germination and, thus, recruitment is also likely to be affected by soil moisture on riverbanks. Priority effects in riparian habitats have been shown to be weaker in wetter conditions (Sarneel *et al.*, 2016), which could mean that over multiple years, native plant communities (especially perennials, like the ones used in this experiment) might become less robust in the face of incoming invasive species.

In conclusion, climate-induced changes in soil moisture in riparian habitats have the potential to be extremely influential in shaping future invasion dynamics along river corridors. Increased precipitation at the beginning of the growth season might favour invasion by certain non-native plant species, such as *H. mantegazzianum*, but different timings and intensities of hydrological processes can also increase the density of native communities or diminish the competitive abilities of all plants, whether they are native or introduced. Results presented here show that native riparian communities growing in favourable conditions which enhance growth are efficient at limiting invasions by non-native species. Understanding these effects, in concert with other environmental factor affecting riparian zones such as land-use and anthropogenic effects, will be key in designing more efficient management strategies in order to control the detrimental spread of non-native species under global climatic changes.

CHAPTER 4

How will future climate change affect the European ranges of the invasive plants *Impatiens glandulifera* and *Heracleum mantegazzianum*?

4.1 INTRODUCTION

Attempting to understand the relationship between the distribution of living organisms within a landscape and the physical environment is an important part of the study of ecology. Species distribution models (SDMs) are numerical tools with a wide variety of applications, which relate species occurrence data with environmental and spatial information (Elith and Leathwick, 2009). An extremely useful application of SDMs is predicting habitat suitability for species under future climate change scenarios, in order to inform conservation and management strategies (Porfirino *et al.*, 2014). Such projections are also often applied in the field of biological invasions, where it is necessary to be able to foresee changes in non-native species' ranges so as to better mitigate their negative ecological and economic impacts (Beerling *et al.*, 1995; *Kriticos et al.*, 2003; Parer-Allie *et al.*, 2009). Models predict expansions and retractions in many non-native plant species' ranges, according to their environmental tolerance levels, leading to difficulties in designing management strategies meant to promote restoration of indigenous communities (Gritty *et al.*, 2005; Bradley *et al.*, 2010).

Historically, despite an increasing interest in the matter, there has been a lack of systematic and comprehensive survey data on species occurrence worldwide, with large databases being compiled opportunistically (Elith and Leathwick, 2009). These records contain a majority of presence-only data, which are characterised by major limitations when attempting to model species distribution, such as decreased result robustness and sampling bias (Phillips *et al.*, 2009). Modelling approaches using pseudoabsence points like MaxEnt (Maximum Entropy) are increasingly used in order to overcome these limitations (Elith *et al.*, 2006). The use of MaxEnt models is exceptionally widespread due to their reduced computational time and simplicity, as well as their ability to model complex relationships between species occurrence and environmental variables, in spite of their shortcomings (Sarikaya *et al.*, 2018; Gebrewahid *et al.*, 2020; *Kaky et al.*, 2020; Du *et al.*, 2021; Cuddington *et al.*, 2022).

As stated in Chapter 1, bioclimatic modelling and manipulative experiments should be employed together more frequently in order to construct a more complete and informative image of biological invasions under climate change (Pattison and Mack, 2007). As observations about competitive outcomes between invasive and co-occurring native species are highly context-dependent and can vary depending on the scale of the study and the species involved, it is crucial to examine multiple facets of these complex relationships (Gonzalez-Moreno *et al.*, 2014; Cabra-Rivas *et al.*, 2016). Here, I will present predictions obtained with the use of MaxEnt models describing the potential future ranges of *Impatiens glandulifera* Royle and *Heracleum mantegazzianum* Sommier & Levier in Europe in the second half of the 21st Century. The projections will cover a larger scale than the previous chapters, which focused on small communities and possible effect of climate change on river corridors alone.

4.2 METHODS

4.2.1 Species occurrence and environmental data

Occurrence data were obtained from the Global Biodiversity Information Facility (GBIF) for both *I. glandulifera* (GBIF.org, 2021a) and *H. mantegazzianum* (GBIF.org, 2021b). Abundance at any given location was not taken into consideration, only the presence or absence – although no absence-only data were recorded. 35,122 distribution points were recorded for *I. glandulifera* and 27,960 for *H. mantegazzianum*. I used six bioclimatic parameters as predictor variables in this study and I selected them from the original Wordlclim dataset of 19 variables (http://www.worldclim.org; Table 4.1) according to their relevance to the environmental variables discussed in Chapters 2 and 3. I chose a resolution of 5 arc-minutes because it is a finer resolution, while still conforming to computer memory constraints. ‘Present’ climate data consisted of a single dataset containing interpolated values from climate data between 1970 and 2000 (Fick and Hijmans, 2017). Future climate data for the 2061-2080 time period were obtained from the 16 climate models under the Coupled Model Intercomparison Project CMIP5 protocol (Taylor *et al.*, 2012) available on the Worldclim website for resolution 5. For CMIP5 I also used two Representative Concentration Pathways: RCP 4.5 (intermediate scenario, with stabilised greenhouse gas emission levels by the end of the century) and RCP 8.5 (pessimistic scenario, with increasing greenhouse gas emissions over time; Wayne, 2013). Mean values for each variable obtained from the 16 climatic models were used in order to build future climate projections (for variability between the climatic models, see Appendices 6-11).

Table 4.1 Set of selected Worldclim bioclimatic variables used to build the models in this study, as well as the results for jackknife test of variable importance in the two models (% contribution).

Variable	Description	*I. glandulifera*	*H. mantegazzianum*
BIO4	Temperature Seasonality (standard deviation x100)	25.8	35.3
BIO5	Max Temperature of Warmest Month (°C)	54.7	43.2
BIO6	Min Temperature of Coldest Month (°C)	10.2	13
BIO15	Precipitation Seasonality (Coefficient of Variation)	7.5	2.1
BIO16	Precipitation of Wettest Quarter (mm)	1.3	6.2
BIO17	Precipitation of Driest Quarter (mm)	0.4	0.2

4.2.2 Model description

Species distribution models were built using the open-source Maxent software V3.4.4 (Phillips *et al.*, 2022). Working parameters were set according to the tutorial available on the Maxent website (Phillips, 2017). In addition, 25% of the occurrence data was selected randomly as the test set used to validate the model (Li *et al.*, 2020; Du *et al.*, 2021). The analysis was carried out by Receiver Operating Characteristic (ROC) and models were evaluated using the area under the curve (AUC). AUC values higher than 0.9 were attributed to extremely accurate models, 0.8-0.9 to highly accurate models, 0.7-0.8 to fairly accurate ones and models with AUC values below 0.6 were considered to have poor performance (Carter *et al.*, 2016). An AUC value of 0.5 indicated a random prediction. Furthermore, for both species I selected jackknife to calculate the importance of each climatic variable (Table 4.1). Habitat suitability under present and future climate scenarios was calculated on a scale of 0 to 1, with 1 representing a completely suitable area and 0 an unsuitable one.

4.3 RESULTS AND DISCUSSION

The AUC values for the MaxEnt models describing *I. glandulifera* and *H. mantegazzianum* distributions were 0.843 and 0.884 respectively, which indicate that the models have a high accuracy when predicting the future ranges of the two species under both emission scenarios examined. Results from an internal jackknife test of variable importance showed that temperature-related variables (temperature seasonality, highest temperature of warmest month and lowest temperature of coldest month) made a considerably greater contribution to the distributions of the invaders than the ones related to precipitation (precipitation seasonality and precipitations of the driest and wettest quarters; Table 4.1). For the *I. glandulifera* model, the cumulative contribution of temperature variables was 90.7%, with the maximum temperature of the warmest months being the most important factor (54.7%). Similarly, in the case of *H. mantegazzianum*, the same variables contributed 91.5% and maximum temperatures of the warmest month having a contribution of 43.2%. Temperature seasonality was also an important factor in the *H. mantegazzianum* model (35.3%), but less so in the *I. glandulifera* model (25.8%). Although possible colinearity between predictor variables has repeatedly been highlighted as a source of uncertainty in species distribution modelling, as climatic variables are often not independent from each other, the performance of MaxEnt models in particular does not seem to be as significantly affected by this shortcoming as other, less complex, models (De Marco and Nobrega, 2018). It is, thus, apparent that increased temperatures could play a great role in shaping European distributions of *I. glandulifera* and *H. mantegazzianum* in the next decades.

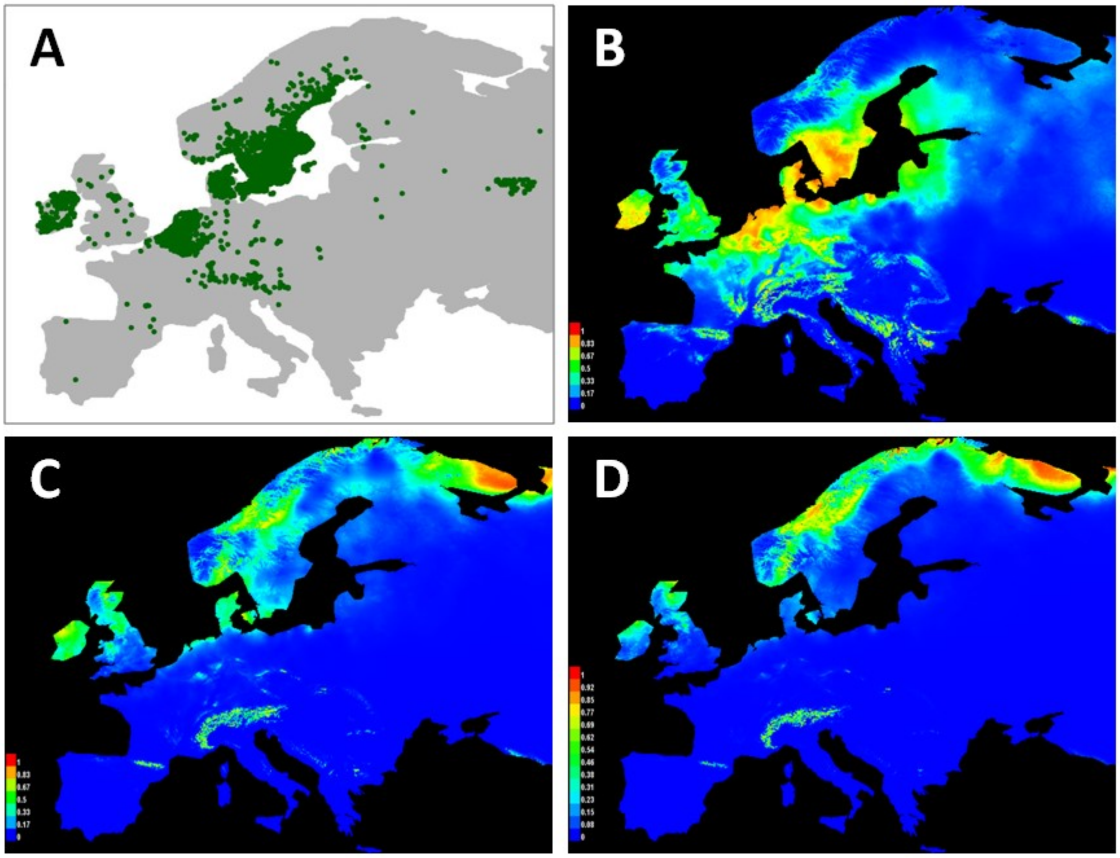

Figure 4.1. (A) Occurrence data for *Impatiens glandulifera* in Europe downloaded from the Global Biodiversity Information Facility (GBIF) databases (1990-2020); (B) Current habitat suitability as predicted on a scale of 0 to 1 by MaxEnt model using climatic variables BIO 4-6 and 15-17 from Worldclim dataset; (C) Future habitat suitability under RCP 4.5; (D) Future habitat suitability under RCP 8.5.

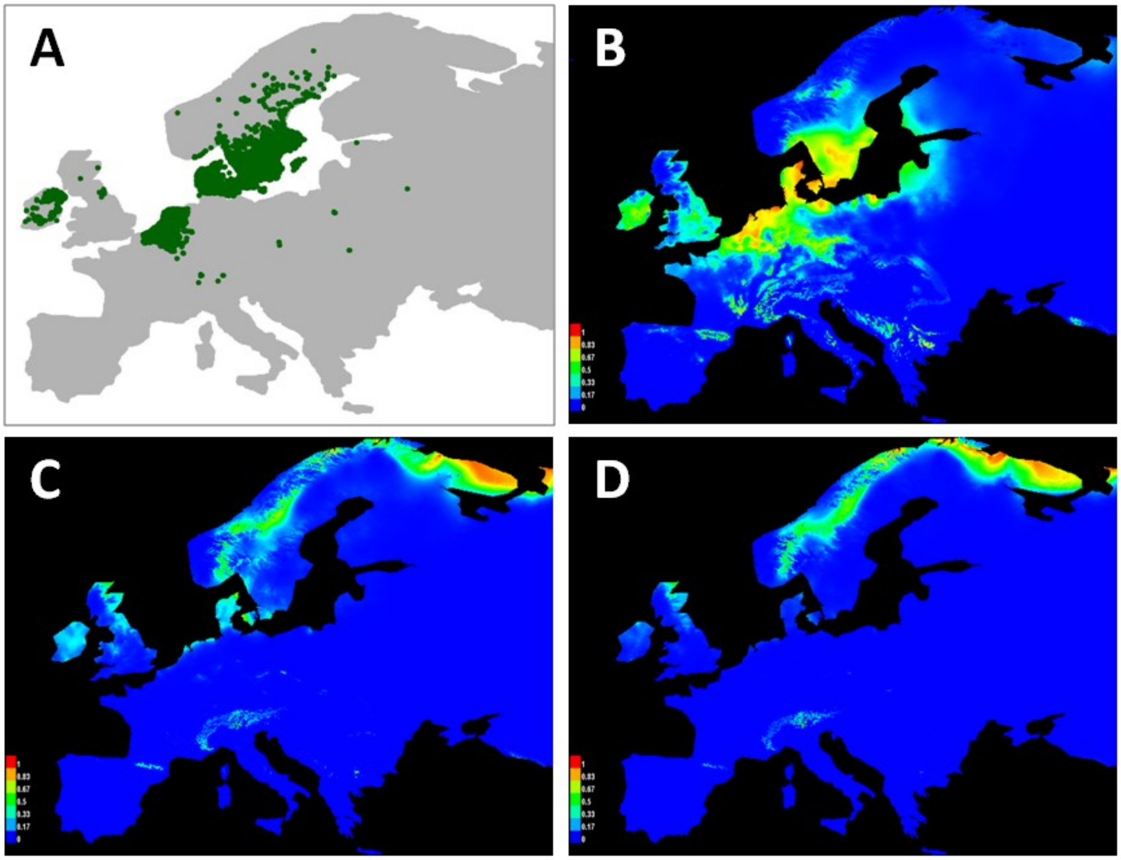

Figure 4.2. (A) Occurrence data for *Heracleum mantegazzianum* in Europe downloaded from the Global Biodiversity Information Facility (GBIF) databases (1990-2020); (B) Current habitat suitability as predicted on a scale of 0 to 1 by MaxEnt model using climatic variables BIO 4-6 and 15-17 from Worldclim dataset; (C) Future habitat suitability under RCP 4.5; (D) Future habitat suitability under RCP 8.5.

Both *I. glandulifera* and *H. mantegazzianum* seemed to have similar current distributions, predominantly with the latter being less abundant and having a smaller range (Figure 4.1, Figure 4.2). Predominantly the invaders have been located in Northwestern regions, as well as mountain ranges in Southern and Eastern Europe. Although this result might be, in part, the product of sampling bias in the occurrence database and limited availability of data from certain European countries, the differences in ranges could be attributed to the fact that *H. mantegazzianum* is a slower moving invader (Wadsworth *et* al., 2002; Cuddington *et al.*, 2022). Nevertheless, experimental evidence suggests that one of the most important factors in limiting the current spread of *I. glandulifera* is temperature, as it more strictly requires higher heat sums (i.e. number of days when temperatures are over 5°C) for germination and survival than *H. mantegazzianum*, and long enough growth seasons for seed production (Willis and Hulme, 2002). The same experiment showed that this is not true to the same extent for *H. mantegazzianum*, which might be more limited by dispersal abilities (Willis and Hulme, 2002).

Ranges seem to be shifting northwards and to higher altitudes under future climate scenarios and Europe generally become less favourable for the invaders. In both the intermediate and the high gas emissions scenarios, Scotland, the northernmost regions of Scandinavia and the Scandinavian Mountains become more suitable for *I .glandulifera*, while the Central and Western European ranges become restricted to high altitude areas in the Alps and Pyrenees (Figure 4.1). Similar shifts occur in the ranges of *H. mantegazzianum*, but the UK seems to become almost completely unsuitable for the species (Figure 4.2). These observations are not surprising, as both species originate from mountainous areas: *I. glandulifera* is native to the Himalayas, while *H. mantegazzianum* is endemic to the Caucasus region.

The models presented here predict that the current ranges of *I. glandulifera* and *H. mantegazzianum* will become less climatically suitable for their establishment and spread. In Chapter 2, I suggested that the invasiveness of *I. glandulifera* could decrease under climate change due to warming-induced changes in phenology, physiology and biomass allocation, making it less competitive against native species. In Chapter 3 I found evidence indicating that drought conditions inhibit the competitive abilities of *H. mantegazzianum*, even when biotic resistance from the native community was low. Higher temperatures could, thus, hinder invasions success for *I. glandulifera* and *H. mantegazzianum* in Europe in the second half of the 21st Century. However, changes in precipitation are likely to have a greater impact in riparian habitats and, thus, on the invasion dynamics of the two species than they seem to do at a larger scale, as water-flow patterns are the main factor shaping riverbank vegetation.

Invaders maintaining a certain level of growth and performance in highly variable conditions, while the performance of co-occurring native species is more closely linked to their environmental context, could prove to be an advantage if fluctuations in resources and disturbance negatively impact their native competitors and increase the invasibility of riparian plant assemblages. Whether this resilience will override the negative impacts of increased temperatures and extreme climatic events will, in all likelihood, depend on the ability of different invasive plants species to manage trade-offs between different physiological and life-history traits which increase their invasiveness under a changing and increasingly unstable climate and the constraints it imposes on plant communities.

The evidence gathered in this thesis indicates that the two main forms of constraint non-native plants are subject to when invading riparian habitats, environmental conditions and biotic interactions, will interact in the future to shape invasion dynamics. The changing global climate is likely to act upon both the external factors, like temperature and hydrological processes, which have the potential to increase or decrease the intensity of plant competition within the community, and the intrinsic plant traits which are involved in determining the outcomes of said competitive interactions. Depending on the identity of the plants themselves, in some areas plant invasions could become an even greater threat to riparian habitats' biodiversity and ecosystem services, but in other areas restoration opportunities may arise. In the near future, riparian invasions could interact with other forms of global change, such as climatic alterations, anthropogenic disturbance and eutrophication, in complex, species-specific and scale-dependent ways which need to be targeted by future researchers more extensively.

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APPENDICES

A.1 Supplementary results for Chapter 2

Appendix 1. Summary statistics for linear mixed models describing the growth of the invasive plant *I. glandulifera* (IG) and three native species (EH = *Epilobium hirsutum*; JV = *Jacobaea vulgaris*; SD = *Silene dioica*) in two different climate conditions (current UK temperatures vs. 3°C warmer), grown in three types of communities (CI = Natives + invader; C = Native only; I = Invader only). Models had time, climate and their interaction as fixed effects and variation at plant level as a random effect and data was natural log-transformed. Effect sizes in bold are associated with insignificant p-values ($P > 0.05$).

Species	Community type	df	Present climate intercept (SE)	Future climate intercept (SE)	Time effect size (SE)	Climate effect size (SE)	Climate x Time effect size (SE)
IG	CI	138	1.805 (0.085)	1.475 (0.085)	0.015 (0.001)	0.027 (0.001)	0.012 (0.001)
EH	CI	124	-1.629 (0.147)	-1.315 (0.147)	0.027 (0.002)	0.032 (0.002)	**0.004** (0.003)
JV	CI	138	-2.194 (0.156)	-2.401 (0.156)	0.035 (0.003)	0.058 (0.003)	0.023 (0.005)
SD	CI	138	-0.713 (0.176)	-1.068 (0.176)	0.030 (0.002)	0.048 (0.002)	0.018 (0.003)
IG	I	138	1.949 (0.086)	1.562 (0.086)	0.013 (0.001)	0.023 (0.001)	0.010 (0.001)
EH	C	138	-1.705 (0.168)	-2.001 (0.168)	0.043 (0.003)	0.060 (0.003)	0.016 (0.004)
JV	C	124	-2.734 (0.209)	-3.011 (0.209)	0.054 (0.004)	0.071 (0.004)	0.017 (0.006)
SD	C	138	-0.638 (0.156)	-1.209 (0.156)	0.046 (0.003)	0.061 (0.003)	0.015 (0.004)

A.2 Supplementary results for Chapter 3

Appendix 2. Summary statistics for post-hoc Tukey's tests comparing soil water content between the baseline watering regime (treatment 2) and the other six treatments. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse. Confidence intervals in bold are associated with insignificant p-values (*P* > 0.05).

PAIR	EFFECT SIZE [CONFIDENCE INTERVAL]		
	Week 2	**Week 5**	**Week 10**
1-2	0.19 [0.10, 0.29]	0.27 [0.14, 0.39]	0.41 [0.21, 0.60]
3-2	-0.24 [-0.33, -0.15]	-0.90 [-1.03, -0.77]	-0.10 [-1.19, -0.81]
4-2	-0.08 **[-0.17, 0.02]**	0.04 **[-0.09, 0.16]**	0.15 **[-0.04, 0.34]**
5-2	-0.10 [-0.20, -0.01]	0.07 **[-0.06, 0.20]**	-0.19 **[-0.38, 0.003]**
6-2	-0.12 [-0.21, -0.03]	0.15 [0.02, 0.28]	0.18 **[-0.02, 0.37]**
7-2	-0.12 [-0.22, -0.03]	-0.23 [-0.36, -0.10]	0.03 **[-0.17, 0.22]**

Appendix 3. Results of ANOVA tests comparing plant height at 3 different time point for four native plant species grown together with *H. mantegazzianum* under 7 different watering treatments.

Species	Week	F	df	*P*
Rumex obtusifolius	**5**	16.39	6	< 0.001
	8	26.50	6	< 0.001
	10	21.80	6	< 0.001
Epilobium hirsutum	**5**	7.26	6	< 0.001
	8	18.71	6	< 0.001
	10	19.62	6	< 0.001
Chamaenerion angustifolium	**5**	4.36	6	0.001
	8	4.21	6	0.001
	10	4.34	6	0.001
Centaurea nigra	**5**	6.18	6	< 0.001
	8	7.41	6	< 0.001
	10	6.08	6	< 0.001

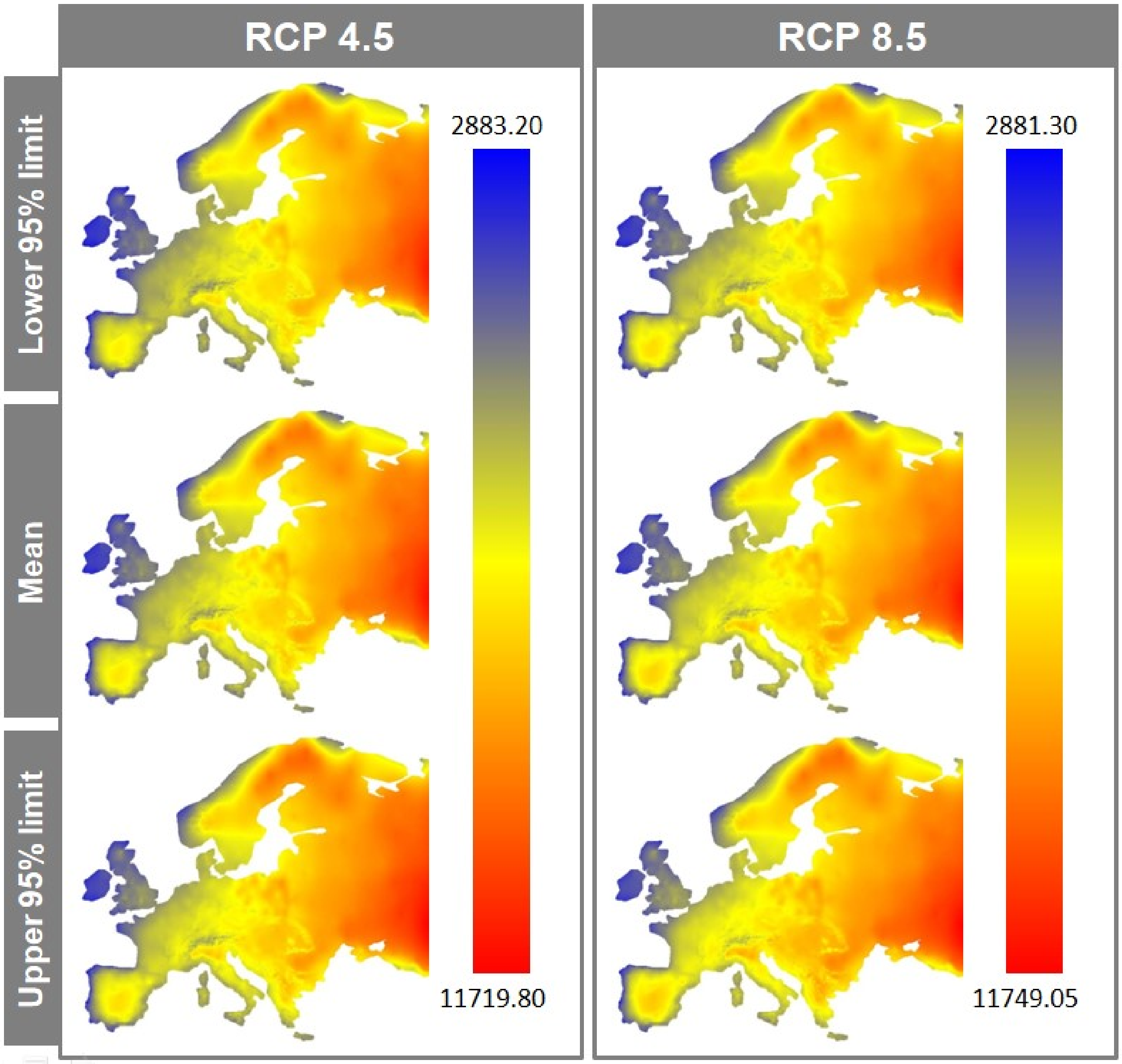
Appendix 4. Summary statistics for post-hoc Tukey's tests comparing plant height at 3 different time points for the invasive plant *H. mantegazzianum,* grown with 4 co-occurring native species, and the best-growing native, *R. obtusifolius*, under 7 watering treatments. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse. Confidence intervals in bold are associated with insignificant p-values ($P > 0.05$).

PAIR	**EFFECT SIZE [CONFIDENCE INTERVAL]**					
	H. mantegazzianum			***R. obtusifolius***		
	Week 5	**Week 8**	**Week 10**	**Week 5**	**Week 8**	**Week 10**
1-2	N/A	-0.32 [-0.60, -0.04]	-0.33 [-0.59, -0.08]	-0.92 [-1.19, -0.65]	-1.17 [-1.44, -0.90]	-1.06 [-1.34, -0.78]
3-2	N/A	-0.48 [-0.76, -0.20]	-0.49 [-0.74, -0.23]	-0.63 [-0.90, -0.36]	-0.60 [-0.88, -0.33]	-0.39 [-0.67, -0.11]
4-2	N/A	-0.01 **[-0.29, 0.27]**	-0.03 **[-0.28, 0.23]**	-0.02 **[-0.29, 0.25]**	-0.01 **[-0.29, 0.26]**	-0.002 **[-0.28, 0.28]**
5-2	N/A	0.01 **[-0.27, 0.29]**	0.03 **[-0.23, 0.28]**	0.12 **[-0.14, 0.39]**	0.12 **[-0.15, 0.40]**	0.19 **[-0.09, 0.47]**
6-2	N/A	-0.20 **[-0.48, 0.08]**	-0.23 **[-0.49, 0.02]**	-0.42 [-0.68, -0.15]	-0.72 [-0.99, -0.44]	-0.65 [-0.93, -0.37]
7-2	N/A	-0.21 **[-0.49, 0.07]**	-0.16 **[-0.41, 0.10]**	-0.14 **[-0.40, 0.13]**	0.04 **[-0.23, 0.32]**	0.13 **[-0.16, 0.41]**
1-4	N/A	-0.31 [-0.59, -0.03]	-0.31 [-0.56, -0.05]	-0.90 [-1.17, -0.63]	-1.15 [-1.43, -0.88]	-1.05 [-1.33, -0.77]
7-4	N/A	-0.19 **[-0.48, 0.09]**	-0.13 **[-0.39, 0.13]**	-0.11 **[-0.38, 0.15]**	0.06 **[-0.21, 0.33]**	0.13 **[-0.15, 0.41]**
3-5	N/A	-0.49 [-0.77, -0.21]	-0.51 [-0.77, -0.26]	-0.75 [-1.02, -0.49]	-0.72 [-1, -0.45]	-0.58 [-0.86, -0.30]
6-5	N/A	-0.21 **[-0.49, 0.07]**	-0.26 [-0.52, -0.01]	-0.54 [-0.81, -0.27]	-0.84 [-1.11, -0.57]	-0.84 [-1.12, -0.56]
7-6	N/A	-0.003 **[-0.28, 0.28]**	0.08 **[-0.18, 0.33]**	0.28 [0.01, 0.55]	0.76 [0.49, 1.03]	0.78 [0.50, 1.06]

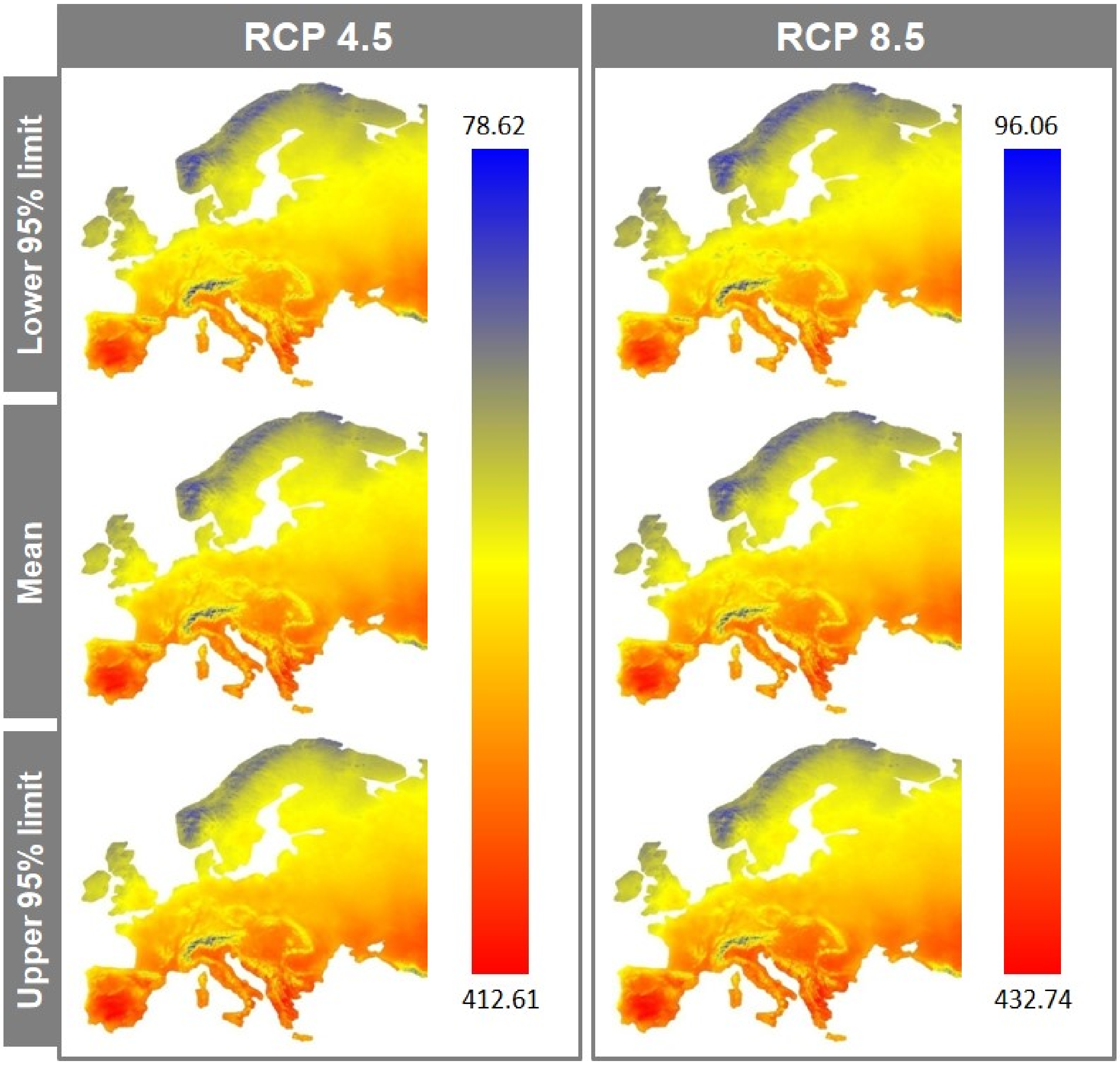
Appendix 5. Summary statistics for post-hoc Tukey's tests comparing the effects of 7 watering treatments, applied for 10 weeks to a community consisting of *H. mantegazzianum* and four native species, on total, aboveground and belowground community biomass and proportional biomass of *H. mantegazzianum*. Treatments are: 1 = constant high; 2 = constant medium; 3 = constant low; 4 = one pulse; 5 = one deficit event; 6 = pulse, followed by deficit; 7 = deficit, followed by pulse. Confidence intervals in bold are associated with insignificant p-values ($P > 0.05$).

PAIR	**EFFECT SIZE [CONFIDENCE INTERVAL]**					
	Total plant biomass			***H. mantegazzianum* proportion**		
	Total	**Above**	**Below**	**Total**	**Above**	**Below**
1-2	-1.89 [-2.51, -1.28]	-1.98 [-2.49, -1.47]	-1.77 [-2.43, -1.10]	2.67 [1.59, 3.75]	2.02 [1.23, 2.80]	2.88 [1.70, 4.05]
3-2	-0.99 [-1.60, -1.28]	-0.76 [-1.26, -0.25]	-1.50 [-2.17, -0.84]	0.41 **[-0.67, 1.48]**	0.69 **[-0.10, 1.48]**	0.83 **[-0.35, 2]**
4-2	-0.36 **[-0.97, 0.26]**	-0.37 **[-0.87, 0.14]**	-0.36 **[-1.02, 0.31]**	-0.21 **[-1.29, 0.86]**	0.69 **[-0.10, 1.48]**	-0.21 **[-1.39, 0.96]**
5-2	0.04 **[-0.57, 0.66]**	0.10 **[-0.41, 0.61]**	0.001 **[-0.66, 0.67]**	-0.31 **[-1.39, 0.77]**	0.14 **[-0.64, 0.93]**	-0.17 **[-1.34, 1]**
6-2	-1.42 [-2.04, -0.81]	-1.52 [-2.03, -1.02]	-1.36 [-2.03, -0.70]	1.42 [0.35, 2.50]	1.82 [1.03, 2.61]	1.34 [0.17, 2.52]
7-2	0.04 **[-0.58, 0.66]**	0.16 **[-0.34, 0.67]**	-0.03 **[-0.69, 0.63]**	-1.16 [-2.24, -0.08]	-0.31 **[-1.10, 0.47]**	-1.94 [-3.11, -0.76]
1-4	-1.53 [-2.15, -0.92]	-1.62 [-2.13, -1.11]	-1.41 [-2.08, -0.75]	2.88 [1.81, 3.96]	1.33 [0.54, 2.11]	3.09 [1.92, 4.26]
7-4	0.40 **[-0.22, 1.02]**	0.53 [0.02, 1.04]	0.33 **[-0.34, 0.99]**	-0.95 **[-2.03, 0.13]**	-1.01 [-1.79, -0.22]	-1.72 [-2.90, -0.55]
3-5	-1.03 [-1.65, -0.41]	-0.85 [-1.36, -0.35]	-1.50 [-2.17, -0.84]	0.72 **[-0.36, 1.80]**	0.55 **[-0.24, 1.3]**	0.99 **[-0.18, 2.17]**
6-5	-1.47 [-2.08, -0.85]	-1.62 [-2.13, -1.11]	-1.36 [-2.03, -0.70]	1.73 [0.66, 2.81]	1.68 [0.89, 2.46]	1.51 [0.34, 2.69]
7-6	1.47 [0.85, 2.08]	1.69 [1.18, 2.20]	1.33 [0.67, 2]	-2.58 [-3.66, -1.51]	-2.13 [-2.92, -1.34]	-3.28 [-4.45, -2.11]

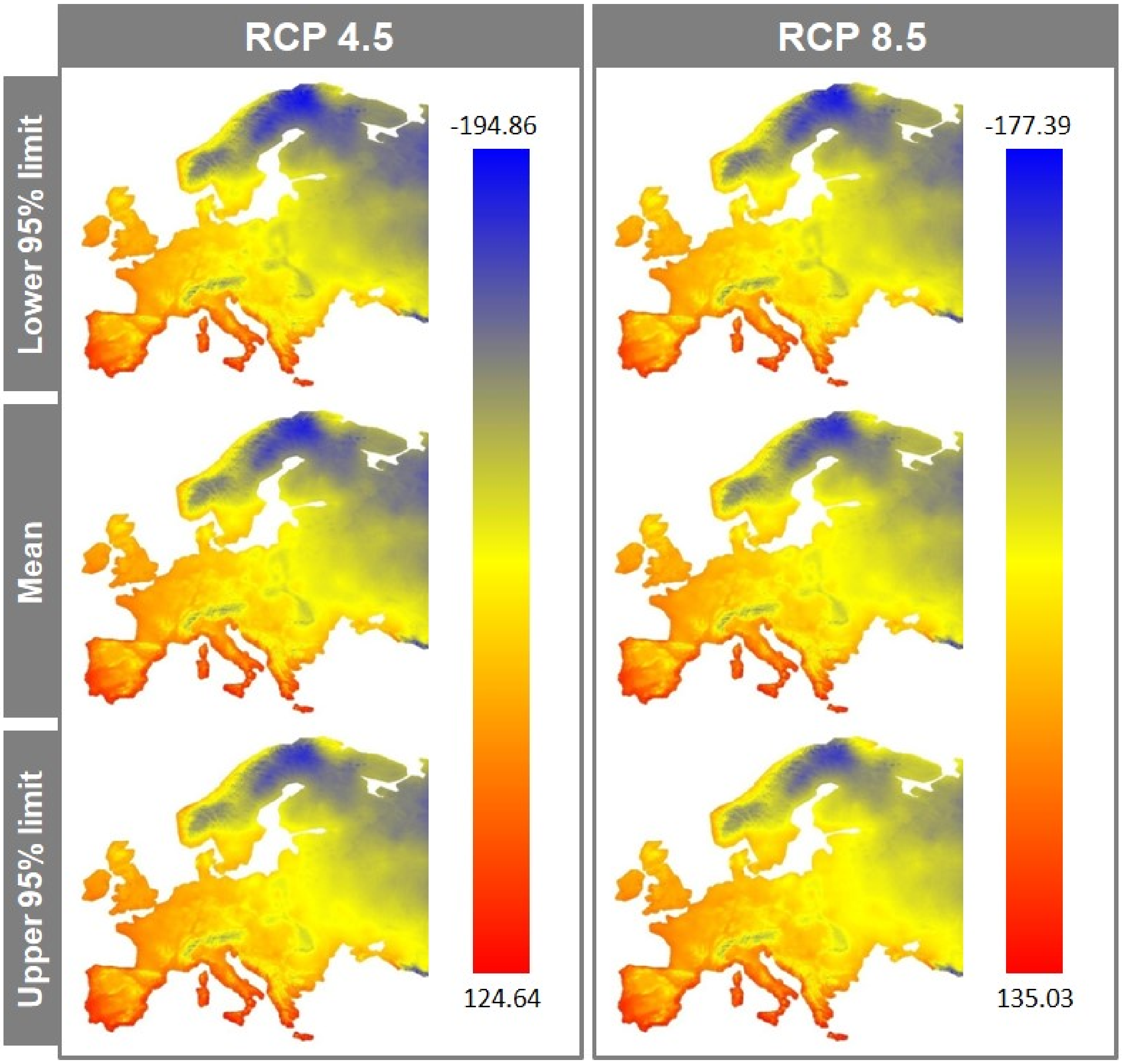
A.3 Supplementary material for Chapter 4



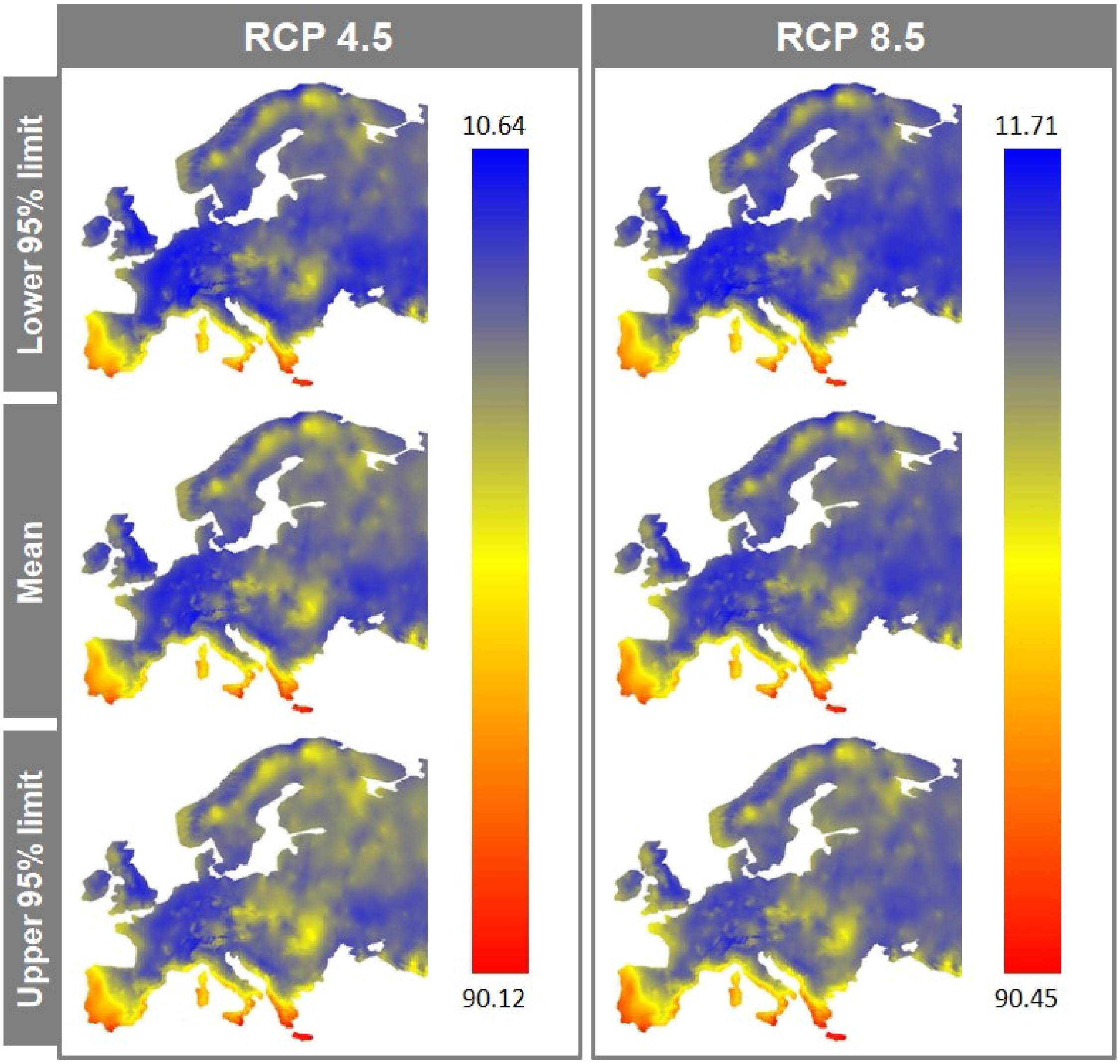
Appendix 6. Mean and 95% limits for temperature seasonality in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).



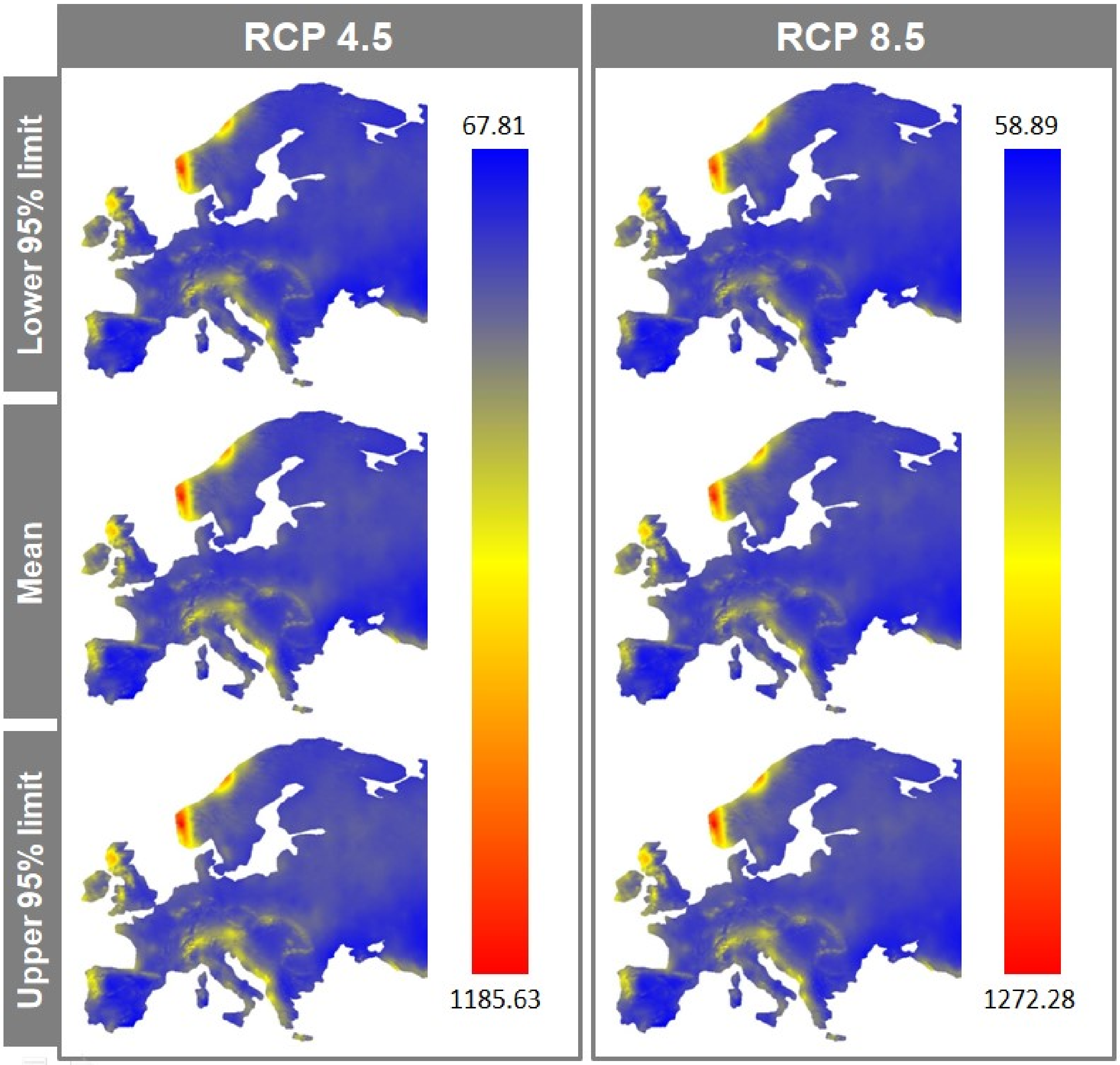
Appendix 7. Mean and 95% limits for maximum temperature of warmest month (°C) in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).



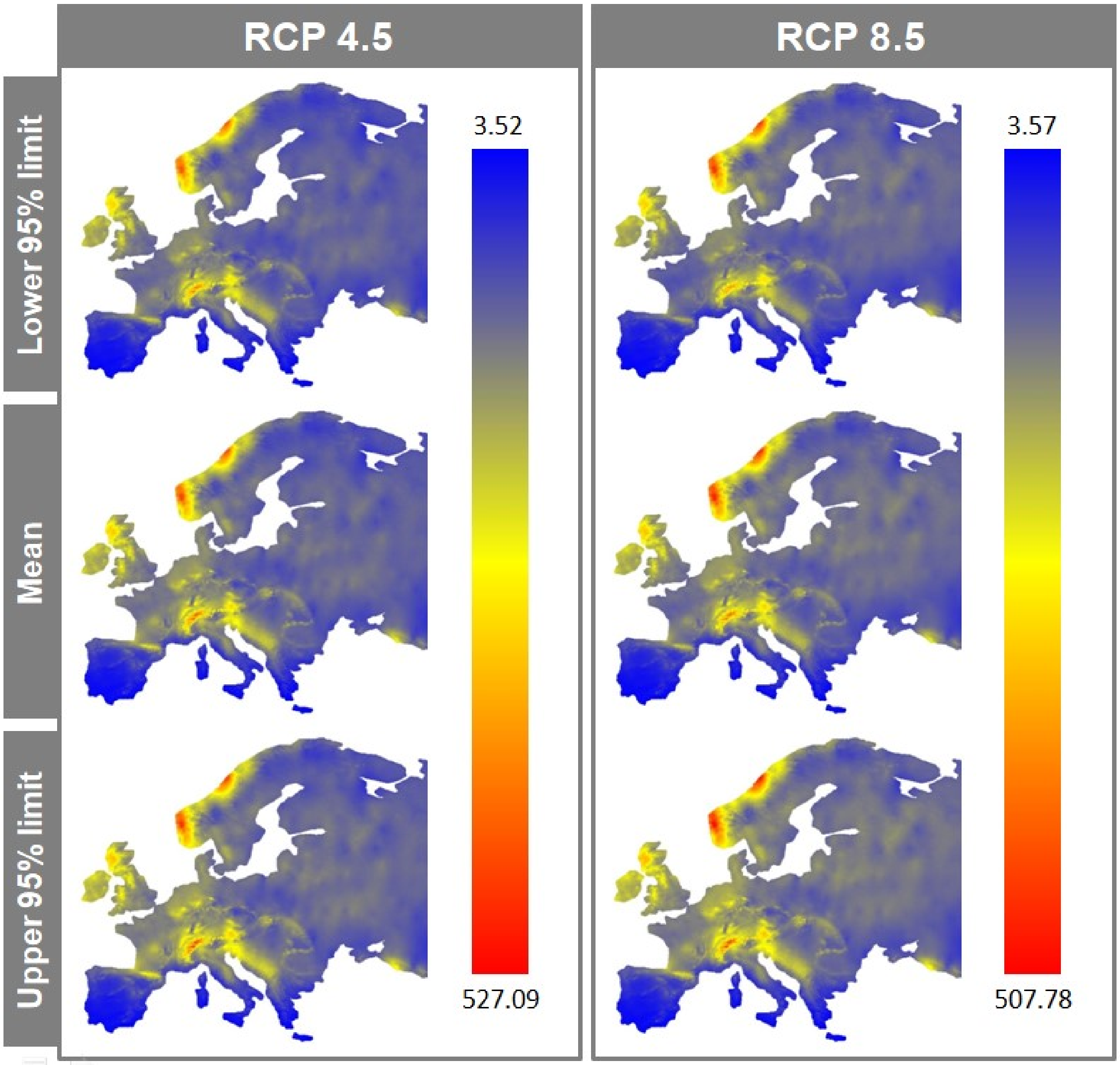
Appendix 8. Mean and 95% limits for minimum temperature of coldest month (°C) in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).



Appendix 9. Mean and 95% limits for precipitation seasonality in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).



Appendix 10. Mean and 95% limits for precipitation of wettest quarter (mm) in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).



Appendix 11. Mean and 95% limits for precipitation of driest quarter (mm) in Europe in the future (2061-2080), obtained from 16 climate models within the CMIP5 protocol, under two Representative Concentration Pathways: 4.5 (intermediate scenario) and 8.5 (high emission scenario).