ABSTRACT

Climate change effects throughout the globe cause increased ecosystem disturbance risk from invasive species. Common St. John's Wort (*Hypericum perforatum*) is a forb native to Europe, Western Asia, and North Africa, and considered an invasive weed in the northwestern United States. *H. perforatum* is present in New England, but appears to be non-invasive. Climate change is highly affecting New England temperatures and precipitation variability, which could have a species-dependent effect on invasives, either facilitating or discouraging invasion. As climate change alters New England climate and ecosystems, the shift in conditions could facilitate *H. perforatum* growth, possibly spurring invasion in New England. This research examines changes in temperature and water availability on *H. perforatum* both alone and combined with competition and disturbance. Water availability was the most important factor in *H. perforatum* germination in this study. Increased temperature facilitated germination when combined with consistent water availability but inhibited germination when combined with variable watering. Disturbance and competition both led to low germination and survival rates although a combination of consistent water and heat increased both. The current climate conditions in New England appear favorable for *H. perforatum* invasion, but non-climate factors likely best explain the current lack of *H. perforatum* invasion.

EFFECTS OF CLIMATE CHANGE FACTORS ON *HYPERICUM PERFORATUM* PRESENCE IN NEW ENGLAND

by

Erin Elizabeth Gerbi

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for eight credits.

This work is dedicated to my brilliant MFS students

for the light and joy they bring to every facet of discovery;

and to Dr. Willie Perreault

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INTRODUCTION

Climate change and human impacts alter biotic and abiotic factors in many regions and ecosystems (Alpert et al., 2000; Sala et al., 2000; Dekker, 2005; Allen & Bradley, 2016; Liu, 2016; Haeuser et al., 2017; Merow et al., 2017; Pearson et al., 2017; Haeuser et al., 2018; Schuster, 2020; Young & Young, 2021; Abbass et al., 2022; Lanta, 2022; Shivanna, 2022; Sun et al., 2024; Miller, 2025). These impacts are wide-ranging and varied but often include damage to native species habitats and lead to loss of biodiversity (Shivanna, 2022), changes in temperature and weather patterns (Young & Young, 2021; Miller, 2025), and increased introduction of biotic material outside of native ranges (Alpert et al., 2000). The resulting impacts of the above effects are often increased invasion vulnerability of affected habitats and ecosystems along with simultaneously increased contact with non-native and invasive species, the combination of which often leads to invasion.

Changing precipitation patterns, warming temperatures, and human disturbance can affect ecosystem health and composition by altering the components and habitability of an ecosystem or habitat to no longer reflect the conditions under which species native to the area have evolved to live. As the surrounding environment shifts, native species may become less suited to their current niche space (Parmesan, 2006; Antão et al., 2022) which may increase native mortality and lead to open niche space in habitats that invaders can capitalize on. Native species frequently lack the level of plasticity and speed of adaptation of similar invasives (Maron et al., 2004; Funk et al., 2008; Droste et al., 2010; Clements & Jones, 2021). Human impacts such as deforestation, harmful agricultural techniques, and biotic exchange can also have a direct impact on ecosystems and habitats (Sala et al., 2000; Abbass et al., 2022).

Response to climate change in native, non-native, and invasive plant species is likely to heavily influence future ecosystem composition. Invasive species have been documented to have more traits increasing competitive ability and resource use efficiency (Godoy et al., 2011; Matzek et al., 2012). The combination of increased competitive ability, resource use efficiency, and plasticity likely increases invasive species resistance to climate change, especially when compared to native species. Data from Haeuser et al. (2017 & 2018) support this idea, finding reduced native competition under climate change (Haeuser, 2017) and superior invasive species performance with increased temperature (Haeuser, 2018). Increased resistance coupled with native decline may lead to increasing invasion risk worldwide as climate change effects increase (Haeuser et al., 2018; Sun et al., 2024).

This research focuses on the possible effects climate change on the germination, performance, and potential impacts of the introduced weed Common St. John's wort (*Hypericum perforatum*) in New England ecosystems. *H.*

perforatum is a notable invader in the western United States (US) but, despite maintaining a self-sustaining population in New England, has not spread rapidly nor become sufficiently widespread or harmful to its surroundings to meet the definition of invasive species.

Defining invasive species

All invasive species are non-native species, meaning they have been introduced to their invasive ranges and maintain self-sustaining populations there (Alpert et al., 2000; Davis & Thompson, 2000; Valery et al., 2008, Clements, 2017; Clements & Jones, 2021). Beyond that, there is a significant amount of disagreement surrounding the definition of invasive species (Valery et al., 2008), largely surrounding if potential or actual harmful impacts should be considered part of the definition. Many non-native species are currently self-sustaining in their non-native regions and do not lead to ecosystem disruption or harm native species. While all invasive species are non-native, not all non-native species meet the definition of invasive.

As defined by Iannone et al. (2020), an invasive species is one that is non-native to the area, has been introduced by human activity, and has the potential to cause or is causing harm to ecosystems, humans, and the economy, while Alpert et al. (2000, p. 53) define an invasive species as “one that both spreads in space and has negative effects on species already in the space that it enters.” Valery et al. (2008, p. 1349) suggest a definition of invasion to consist of “a species’ acquiring a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population.” Combined, definitions of invasion and invasives suggest invasive species must be both non-native to an area and aggressively or rapidly spreading, and in addition typically cause harm to the surrounding ecosystem (Alpert et al., 2000; Davis et al., 2000; NOAA, 2019; Iannone et al., 2020). While impact or harm is not always an explicit factor in defining an invasive species (e.g. Valery et al., 2008; Guiaşu and Tindale, 2023), many of the factors within the defining criteria (e.g. aggressive spread) are implicitly harmful to invaded ecosystems, habitats, or communities (Davis & Thompson, 2000; Valery et al., 2008; Iannone et al., 2020).

When discussing potential definitions of invaders, we must be careful not to miss the forest for the kudzu-covered trees and disregard the tangible ecosystem impact of aggressively spreading non-native species. Invasive species are adept at slithering into unoccupied niches (Davis et al., 2000; Clements & Jones, 2021), frequently overtake and “choke out” native species, and often cause widespread ecosystem disruption, depletion of soil nutrients, and significant reductions in biodiversity (Carlyle et al., 2014; NOAA, 2019; Shivanna, 2022). Invasion also appears to facilitate invasion (Sun et al., 2024), increasing ecosystem vulnerability. In this research, an invasive species is considered to be one that has widespread and rapidly spreading self-sustaining populations in a non-native range and may be detrimental to the surrounding habitat, ecosystem, or environment.

It is important to note that the classification of invasive species is dependent on geographical region and local ecosystems. An organism or plant considered to be invasive in one region may be native to another, and non-native non-invasive in a third. We do not consider plants that have established themselves outside of their native range as a result of climate change mediated range shifting to be inherently invasive; however, they may become invasive as a result of climate or weather events, changes in predation or fitness within the new range, or plasticity (Alpert et al., 2000; Finch et al., 2021). A species considered to be non-native and non-invasive may still cause ecosystem harm and decrease native populations in a manner similar to an invasive species, even without achieving the widespread impact of invasive species (Alpert et al., 2000). Non-native plants may outcompete their native counterparts without mounting a full invasion of an ecosystem, or a change in environmental factors such as precipitation, temperature, or disturbance may allow non-natives to take over an area without being initially considered invasive (Alpert et al., 2000; Finch et al., 2021).

Common traits and aspects of invasive species and factors indicated their spread

Although there is no list of defining traits found in all invasive species, there are several traits common to many invasive species. Many invasives have common traits that allow them to spread, reproduce, and adapt to ecosystem changes (Willis et al, 2010; Godoy, 2011; Matzek, 2012; Kiesel, 2014; Xavier et al, 2017; Clements & Jones, 2021), which helps give an idea of how invasive species are able to invade and establish in ecosystems as well as the risk factors that lead to species either native or introduced becoming invasive. Traits increasing invasion capability frequently center around an ability to adapt to a wide variety of climate and ecosystem conditions, rapid growth, and increased competitive advantage (Maron et al., 2004; Dekker, 2005; Willis et al., 2010; Godoy, 2011; Matzek, 2012; Molins et al., 2014; Lustenhouwer et al., 2017; Xavier et al., 2019; Clements & Jones, 2021).

Phenotypic plasticity, a shifting in an organism's displayed traits in response to environmental stimulus without changes to its genetic code, is theorized to play a major role in allowing invasive species to expand beyond their introduced ranges and spread in a wide range of new or changing environments (Willis et al., 2010; Xavier et al., 2019; Lustenhouwer et al., 2017; Clements & Jones, 2021). Many invasive species are able to exhibit phenological traits such as flowering or germination time to increase their fitness within a new habitat without any genetic change or difference from other members of their species in separate environments and/or different ranges (Willis et al., 2010; Xavier et al., 2019). In addition to phenotypic plasticity, reproductive plasticity, such as a single species having the ability to reproduce either sexually or by self-fertilization, may be an important factor in initial invasion by allowing reproduction without high population numbers or density during early stages but also permitting genetic recombination and diversity during later stages (Maron et al., 2004; Molins et al., 2014; Clements & Jones, 2021).

Along with forms of plasticity, rapid local or population level adaptation allows the same or similar invaders to colonize wide varieties of habitats and ecosystems (Maron et al., 2004; Lustenhouwer et al., 2017; Williams et al., 2016; Finch et al., 2021). Unlike phenotypic plasticity, local adaptation is the result of genetic changes due to selective pressures. Locally adapted species are distinct from other populations in geographically separated ranges (Beckmann, 2011). Many invasives show evidence of adaptation to introduced ranges on shortened timescales (Lustenhouwer et al., 2017; Clements & Jones, 2021), allowing them to quickly increase fitness for their introduced range and niche and better equipping them to adjust to gradual environmental changes over generations. Rapid evolution will likely play an increasingly important role in the continued survival and range expansion of invasive species as climate change continues to alter ranges and ecosystems (Williams et al., 2016; Lustenhouwer et al., 2017; Clements & Jones, 2021).

Rapid growth rates allow invasives to outcompete surrounding native species for resources such as sunlight, water, and soil nutrients (James & Drenovsky, 2007; Betekhtina et al., 2019) and more quickly establish and/or reestablish themselves in cases of disturbance (Dekker, 2005; Maron et al., 2004; Dlugosch et al., 2015). There is also some evidence that invasive species have higher resilience following drought or disturbance (Barros et al., 2020; Clements & Jones, 2021).

Although individual organism and species traits are important, external factors may play a similar or greater role in determining invasion capability. The Enemy Release Hypothesis (ERH) suggests that invasive plants may gain dominance in their invasive range as a result of newfound freedom from predators or consumers in their native ranges (Elton 1958). ERH has been theorized to give an edge to invasive species because native species experience greater predation (Elton, 1958; Maron and Marler, 2008; Zhang et al, 2018). ERH goes hand-in-hand with the Evolution of Increased Competitive Ability (EICA) hypothesis, which postulates that invasive species are able to switch resources previously used for defense against predators in their native range to growth and reproduction, thus leading to their ability to outcompete native plants (Blossey and Nötzold, 1995). These effects are also theorized to be a reason why previously non-invasive species may suddenly become invasive in their introduced range (Flickinger and Dukes, 2024).

It is important to note that while ERH and EICA appear to explain many reasons for sudden and aggressive dominance of invasive species, they do not apply universally (e.g. Colautti et al., 2004; Van Kleunen and Shmid, 2003). EICA in particular appears to have limited ability to explain invasive species ability to establish and dominate an ecosystem (Callaway and Ridenour, 2004; Felker-Quinn et al., 2013), and further examination has not strongly supported Blossey and Nötzold's 1995 claim (Van Kleunen et al, 2003; Callaway and Ridenour, 2004; Felker-Quinn et al., 2013). Colautti et al. (2004) found that ERH was generally supported in over half the predictions studied, but emphasized the importance of other factors possibly contributing to the success of invasives. Prior et al. (2015) found convincing evidence for ERH lacking, and supported Colautti et al.'s (2004) conclusion of need for further research with wider scope.

Although the above traits are frequent predictors of invasion capability within a species, many traits that make a species invasive are habitat dependent. The final say in if a species is able to invade a habitat or ecosystem rests on the match between the habitat or ecosystem's composition, climate, and history with the traits of the invader.

Invasion-vulnerable habitats and ecosystems

Habitat invasion is typically driven by a combination of an available invader and a habitat with one or more factors that increase its vulnerability to invasion (Alpert et al., 2000; Davis et al., 2000; Finch et al., 2021). Combinations of low biodiversity, high resource availability, and high non-natural disturbance – such as grazing – have been shown to be important factors in predicting an ecosystem's susceptibility to invasion (Davis et al., 2000; Fensham et al., 2011; Dlugosch et al., 2015; Cao et al., 2024). Previously invaded environments also appear to have a higher risk of invasion (Sun et al., 2024).

Native biodiversity and establishment along with overall ecosystem composition have strong effects on the invasibility of a habitat or ecosystem (Fern et al., 2010; Sun et al., 2024). High biodiversity and lack of disturbance are two factors correlated with reduced invasion risk in grasslands (Hector et al., 2001; Gelbard and Harrison, 2005; Fern, 2010; Yanelli et al., 2017; Yanelli et al., 2020; Cheng et al., 2024; Sun et al, 2024). This effect holds true even under climate change, with high levels of grassland biodiversity demonstrating stronger defense against invasion under overlapping warming and drought conditions (Cheng et al., 2024), and low biodiversity leading to increased drought damage (Smith, 2024).

Ecosystem composition is a major factor in a habitat's ability to resist invasion (Maron & Marler, 2007), and may play a major role in how and to what degree an ecosystem's invasibility will be affected by climate change (Pearson et al., 2017; Arias et al., 2023; Flickinger and Dukes, 2024). Ecosystems with higher proportions of native species may have higher resistance to invasion, and high biodiversity may be associated with protection against other climate change events, such as erosion due to flooding (Firn et al., 2010; Sun et al., 2024) which cause direct ecosystem damage and increase vulnerability to invasion.

Ecological disturbance, as defined by White and Pickett (1985, p. 7) is "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment". Disturbance can have destabilizing effects on ecosystem structure (Collins, 2000), frequently leads to a loss of biodiversity (Turner, 2010), and can permanently alter ecosystem composition (Turner, 2010). When discussing disturbance as a factor in invasion vulnerability, it is important to note that not all forms of disturbance are detrimental to an ecosystem, and many are essential to maintaining both ecosystems as a whole and individual components (Davies et al., 2009; Turner, 2010; Newman, 2019). These "historical disturbances" or "natural disturbances", such as wildfires in chaparral forests, frequently increase ecosystem resistance and can defend against invasion – few invasives are as well-suited to establishing in such an environment as native species (Davies et al., 2009; Newman, 2019). Disturbances that diverge from historical patterns are frequently the most harmful – the further from typical the disturbance, the more likely it is to cause harm and long term or permanent disruption to an ecosystem (Davies et al., 2009)

Hand-in-hand with disturbance, competition and resource availability are highly important factors in a community's resistance or lack thereof to invasion (Gelbard & Harrison, 2005; Firn et al., 2010; Pearson et al., 2017; Arias et al., 2023). Established populations may be able to repel invaders under reduced resource availability (Pearson et al., 2017; Cheng et al., 2024), and Arias et al. (2023) observed the detrimental effect of invasive species on native populations to be higher with increased resource availability. Lower resource availability appears to under some circumstances be beneficial to established native communities in resisting invasion. Firn et al. (2010) found evidence for invasive repulsion under high resources in an established native community and suggested previous establishment to be the greatest factor in invasion resistance. Evidence from Yanelli et al. (2017, 2020) support pre-established native communities to be instrumental in resisting invasion and suggest available resource reduction via the establishment of fast growing natives in open niches as a possible restoration strategy. A combination of low biodiversity, high non-natural disturbance, and high resource availability appears ideal for invasive species establishment.

Global change, climate change, ecosystem impacts, and invasion

Global change describes alterations in interactions between the natural environment and its inhabitants via human activity across space and time (Tanentzap & Kolmakova, 2023). Events such as the introduction of species outside of their native range, land alteration such as for grazing, logging, or cropping, and pollution are all considered aspects of global change (Sala et al., 2000; Vila et al., 2011; Salonen & Reiser, 2023; Tanentzap & Kolmakova, 2023).

A major factor of global change affecting ecosystem biodiversity and resources is climate change. Climate change is defined by Solonen and Reiser (2023, p. 565) as “a measurable systemic change in the state of the climate driven by natural events or anthropogenic activities that alter the composition of the atmosphere” and is a major factor in current ecosystem decline (Clements & Jones, 2021; Shivanna, 2022; Salonen & Reiser, 2023; Flickinger & Dukes, 2024). The term climate change encompasses climate events such as shifts in precipitation or other weather patterns, temperature changes, and extreme weather events that may cause floods and wildfires (Abbass et al., 2022; Salonen & Reiser, 2023). The type, frequency, and severity of these effects is dependent on geographic location (Bahlai et al., 2021).

In response to climate change, the areas in which many species live and establish are changing. Clements and Jones (2021) suggest major factors in climate change-mediated invasive species spread will be range shift and expansion towards the poles due largely to warming temperatures and increased introduction and establishment to new regions due to extreme weather events (e.g. floods). Extreme weather events may also result in significant ecosystem disturbance (Burton et al., 2020; Walsh et al., 2020), which may damage or destroy previously habitable ecosystems in addition to introducing non-native species (Haeuser et al., 2018; Clements & Jones, 2021; Flickinger & Dukes, 2024; Sun et al., 2024). The effects of climate change are varied across space and environment, but are nearly always harmful to native populations and ecosystems (Beyen & Jain, 2015; Liu, 2016; Haeuser et al., 2017; Haeuser et al., 2018; Spinoni et al., 2018; Hess et al., 2019; Bahlai et al., 2021; Descamps et al., 2021; Young & Young, 2021; Abbass et al., 2022; Smith et al., 2024; Sun et al., 2024).

Global and climate change factors are having significant impacts on ecosystem health and invasive species establishment by reducing native biodiversity as a result of lost niche space and fluctuating resources (Hess et al., 2019; Shivanna, 2022; Smith et al., 2024) and increasing disturbance, which may simultaneously reduce native density and introduce invasive species to a now vulnerable habitat or ecosystem (Burton et al., 2020; Walsh et al., 2020; Clements & Jones, 2021). Temperature and precipitation variance are increasing globally (Spinoni et al., 2018; Descamps et al., 2021; Robinson et al., 2021), as are extreme weather events (Robinson et al., 2021; Marvel et al., 2024; Yu et al., 2024).

Both climate change and global change contribute to invasive species introduction and establishment (Davies et al., 2009; Allen & Bradley, 2016; Merow et al., 2017; Newman, 2019; Schuster et al., 2020; Lanta et al., 2022; Tanentzap & Kolmakova, 2023). As ecosystems continue to be altered as a direct result of climate change, traits responsible for the success of invasive species such as increased plasticity and rapid evolution may allow for better adaptation and survival than their native counterparts, leading to increased invasion potential. Studies by Willis et al. (2010), Kiesel (2014), and Xavier et al. (2017) suggest that most native species will be less able to adapt to or withstand changing precipitation, temperature, and weather patterns than their invasive and non-native counterparts, leading to a possible increase in comparative competitive ability allowing invasive plants to outcompete previously resistant natives. Their findings are supported by Haeuser et al., (2017, 2018), who suggest invasive species performance under climate change would improve relative to native performance. Rapid evolution and phenotypic plasticity may also play a role in allowing invasive species to adapt to climate change more rapidly than native communities (Clements & Jones, 2021)

Climate change may drive range expansion for invasive species more rapidly than native species (Lustenhouwer et al., 2017; Clements & Jones, 2021). With rapidly increasing range, both documented invasive species and introduced species can become threats. Introduced species, even if not invasive in other or previous introduced or native ranges, can become invasive threats if they suddenly are no longer in conditions suppressing their growth or reproduction (Clements & Jones, 2021). Predation, consistent disturbance, and climate constraints all could prevent a species from invading. When introduced to a new range free of such threats, said species may be able to establish, grow, and reproduce at rates within its introduced ecosystem that lead to it being considered invasive (Flickinger & Dukes, 2024). However, much range shifting is in itself simply a response to changing climate conditions, particularly temperature, and does not indicate invasion potential (Clements & Jones, 2021; Flickinger & Dukes, 2024).

Both global change and climate change have been documented to reduce biodiversity and biomass in ecosystems (Carlyle et al., 2014; Shivanna, 2022; Tanentzap & Kolmakova, 2023). This reduction in biodiversity has been shown to increase habitat invasibility by leaving open niches that can then be occupied by fast-establishing invaders (Dlugosch et al., 2015). As earlier mentioned, previously established native species populations may be able to repel invasive attempts at establishment; this ability is often diminished with increasing ecosystem disturbance and loss of resources (Maron & Marler, 2007; Firn et al., 2010; Vila et al., 2011; Pearson et al., 2017; Arias et al., 2023, Sun et al., 2024). The disruption of ecosystems and native species is both a cause and effect of climate change, creating a vicious cycle of invasion and loss of biodiversity. Incidents of climate driven range shifting and climate change mediated invasion have increased steadily over the past decades (Flickinger & Dukes, 2024; Clements & Jones, 2021). As incidents of extreme weather events have been increasing rapidly over the past decades as well (Marvel et al, 2024; Yu et al, 2024), it is likely that invasions as a result of extreme weather events and other climate change factors will continue to increase.

Geographic location is an essential factor in determining which effects of climate change will be most keenly felt, as well as the severity of those effects. Northern forests are considered more likely to have extreme effects from warming in particular, along with drought and extreme weather events (Newman, 2019; Bahlai et al., 2021), and are particularly vulnerable to disturbance (Schuster et al., 2020; Lanta et al., 2022). Geographic location is most important in determining abiotic effects of climate change, although it still influences biotic factors, typically by determining original ecosystem composition and creating range limitations on invasive or introduced species (Newman, 2019).

It is important to note that there are areas in which climate change reduces invasion risk (Allen & Bradley, 2016; Evans et al., 2023), and that factors such as human disturbance can have similar effects on native and invasive species or even be detrimental to invasives (Lear et al., 2022). However, despite there being circumstances in which invasives are delayed or stymied by climate change, the majority of climate change factors facilitate invasion, frequently through range expansion (Lustenhouwer et al., 2017; Flickinger & Dukes, 2024), ecosystem disturbance (Lear et al., 2022), or precipitation pattern changes (Xavier et al., 2019).

Hypericum perforatum and Hypericum punctatum

Hypericum perforatum, known as St. John's wort or Klamath weed, is a perennial forb native to shrub and grasslands in Europe, Western Asia, and North Africa. In its introduced range, it frequently occurs in grassland and pasture areas, and can also be found at forest edges and clearings, preferring full sun and low competition (Zouhar, 2004). *H. perforatum* tends to be branchy and reach an average height of 0.5m and is typically no more than 1.5m tall, although in some parts of the western US coast it may grow up to 2m (Randall, 2018). Flowers are small and yellow, approximately 2.5cm across. Flowering typically occurs June through September in US ranges (Reeves, 2010). *H. perforatum* may form dense vegetative stands of crowns connected by a single root system, which contributes to its ability to crowd out nearby native species (Zouhar, 2004). Mild disturbance appears to be highly favorable to *H. perforatum* establishment, but high disturbance is effective at mitigating invasion (Davey, 1921 via Harris & Gill, 1997). *H. perforatum* grows relatively slowly, and has a low drought tolerance (Zouhar, 2004).

Figure 1. Image of flowering *Hypericum perforatum*. Rice via Zouhar, (2004)

The first recorded introduction of *H. perforatum* to North America was in Pennsylvania in 1793 (Vila et al., 2003). It has been introduced multiple times since then (Vila et al., 2003), likely for cultivation for medicinal purposes (Walker et al., 2001). Since its introduction, *H. perforatum* has spread throughout many regions of North America (Zouhar, 2004). *H. perforatum* causes photosensitivity when ingested, which is especially impactful to livestock as pasture habitats appear to be a prime habitat for *H. perforatum* (Sheahan, 2012). Impacts on livestock and pasture along with rapid spread have led *H. perforatum* to be classified as an invasive species in the northwestern US and Canada (Williams, 1984; Harris & Gill, 1997; Walker, 2001; Zouhar, 2004; Sheahan, 2012). *H. perforatum* is also non-native to the midwest and northeastern regions where it has established but does not seem to spread as aggressively or have major impacts on native species or communities with less virulence (Maron et al., 2004; Morrison et al., 2017). Currently, there are multiple distinct populations of *H. perforatum* within North America and the United States (Buckley et al., 2003; Barcaccia et al. 2006).

H. perforatum growth may be hindered by competition with surrounding grass (Willis et al., 1998 via Buckley et al., 2003), and water stress (Buckley et al., 2003), and so appears to invade most effectively in disturbed grasslands with high water availability. *H. perforatum* tends to germinate during the rainy or wet seasons in its invasive ranges (Zouhar, 2004; Beckmann, 2011), appearing highly responsive to water availability. High soil moisture appears required for optimal growth, seed production, and germination (Campbell, 1985), although specific soil moisture requirements are somewhat unclear (Zouhar, 2004). Harris (1951) estimates *H. perforatum* to require between 89-102 cm of rainfall per year in its introduced ranges. However, when precipitation is in the form of snow, *H. perforatum* may only require 25-30 cm of precipitation annually (Harris, 1951).

Germination behavior may be population specific and populations demonstrate local adaptation, although germination during the rainy or wet seasons of the invaded region appears consistent (Pérez-García et al., 2006; Beckmann et al., 2011) . Early studies by Pritchard (1960) appeared to support increased competitive ability in *H. perforatum* populations in their introduced range. Vila et al. (2003) and Maron et al. (2004), found this conclusion lacked support, and suggested phenotypic plasticity and high genetic variability between regional populations was a more important factor facilitating *H. perforatum* invasion capability. *H. perforatum* may lie dormant in seed banks for long periods of time, then germinate and grow following disturbance to the area (Warr et al., 1994; Coates, 2008). Seed bank presence appears to be maintained even with a lack of vegetation (Zouhar, 2004; Coates, 2008).

In addition to *H. perforatum*, New England is home to several native species of *Hypericum*. *Hypericum punctatum* (Spotted St John's wort) is native to northern New England and highly similar to *H. perforatum*. *H. punctatum* is not considered to be invasive in any regions of the US (USDA, 2024). *H. punctatum* displays similar morphological characteristics and habitat preferences to *H. perforatum*.

Figure 2. Image of *Hypericum punctatum*. Randall, (2024).

Coates (2008) found *H. punctatum* to be absent from the seed bank in several sites surrounding the Quabbin Reservoir in western Massachusetts (MA), and a high presence of *H. perforatum*. *H. punctatum* was also absent from sites where it had previously been found, and was not present in any sites where *H. perforatum* was present (Coates, 2008). The apparent decline in *H. punctatum* populations, especially in areas with *H. perforatum* presence, may indicate *H. perforatum* to be highly impacting *H. punctatum* populations even in a region where *H. perforatum* is not considered invasive.

H. perforatum in New England ecosystems

New England lies in a temperate forest biome located in the northern hemisphere. Temperate forest ecosystems may be more vulnerable to precipitation variability and global change effects such as disturbance (Gilliam, 2016; Schuster et al., 2020; Bahlai et al., 2021; Lanta et al., 2022). New England is heavily forested and has limited open grassland (Foster, 1992; Johanson et al., 2016; Bahlai et al., 2021). Strongly established native populations and high biodiversity likely play a significant role in increasing invasion resistance of temperate forests (Gilliam, 2016; Schuster et al., 2020; Bahlai et al., 2021; Lanta et al., 2022). As a result of reforestation and conservation efforts following rapid deforestation through the mid-19th century, total forest area in New England peaked in the 1980s and is now in decline (Bahlai et al., 2021).

Sala et al. (2000) theorized the likely impacts of climate change on northern temperate forests would be focused around factors affecting wide areas of the globe such as increasing temperature and precipitation variability, which appears to be supported (Young & Young, 2021; Miller, 2025). The summer of 2024 was the hottest year on record (Miller, 2025) and winter temperatures are rising, causing lower snowfall and earlier icemelt (Beyen & Jain, 2015; Miller, 2025). In the future, northern temperate forests are predicted to have a warmer and drier climate across the board, with decreasing precipitation frequency year-round and lower accumulation of snow in the winter months (Rustad et al., 2011; Beylen & Jain, 2015; Young & Young, 2021). In addition, species native to more southern areas of the region are expected to shift northward (Bradley et al., 2010; Merow et al., 2017).

New England summers are warm, with average summer temperatures ranging from 19-22°C and an average maximum temperature of approximately 27°C (NOAA, 2024), and wet, with a three-decade precipitation average of approximately 84cm (NOAA, 2024). Winters average approximately 90cm of snowfall (NOAA, 2024). New England temperatures appear to be viable for *H. perforatum* invasion, and New England has sufficient rain and snowfall to support *H. perforatum* germination. Industry and land use in New England often create open and disturbed spaces such as those preferred by *H. perforatum* (Foster, 1992; Gilliam, 2016), but the region appears to remain less than ideal for wide-scale invasion. Most of New England's natural spaces are still forested, and much of the cleared and undeveloped non-forest land in New England is cropland (Foster, 1992; Johanson et al., 2016), both of which could limit *H. perforatum* presence and invasiveness in New England as a whole.

Hypotheses

I examined the effects of both ambient and warmed temperature combined with consistent or variable watering, and varying amounts of competition and disturbance. Pots within the temperature and water treatments were randomly assigned to treatments involving disturbance and/or competition with wheatgrass. *H. perforatum* was seeded into pots either with undisturbed pre-established wheatgrass competition, disturbed pre-established wheatgrass competition, or no competition. Following germination, half of the germinated seeds in each treatment were then disturbed.

H. perforatum appears to be affected most by water availability and competition, the effects of which may be influenced by temperature and disturbance. Given the available research, I predicted that *H. perforatum* would struggle to establish itself in undisturbed areas with competition, but fare better with prior disturbance. I also predicted heat would increase *H. perforatum's* ability to establish itself both with and without disturbance, with the highest rate of germination and growth with a combination of disturbance and heat, and that water availability would enhance its germination and growth rates. I further predicted that post-planting disturbance would reduce *H. perforatum's* survival rate, and that this effect would be slightly reduced in pots with both warmed temperatures and consistent watering. Lastly, I predicted that all pots in the warmed temperature treatment would perform better than their counterparts in the ambient treatment, regardless of water variability.

METHODS AND MATERIALS

For this research, a greenhouse experiment with combinations of warming, competition, disturbance, and water variability treatments was conducted from October 2024 to January 2025. A total of 192 8.9cm^2 pots were used. Each treatment contained 8 replicate pots with six *Hypericum perforatum* seeds in each pot. Germination was followed from November to December 2024 and growth was measured from December 2024 to January 2025.

Pots were randomly divided into ambient or warmed temperature and consistent or variable watering, which overlapped to form four distinct treatments: ambient temperature and consistent water (AC), warmed temperature and consistent water (WC), ambient temperature and variable water (AV), and warmed temperature and variable water (WV). Pots were then randomly divided into initial planting conditions of competition with undisturbed wheatgrass, competition with disturbed wheatgrass, and no competition. Following this arrangement, half the pots within each initial planting condition were randomly placed in either the post-germination disturbance treatment or the no post-planting disturbance treatment. This distribution was later adjusted to account for low germination rates, but the proportion of pots within each treatment remained roughly the same.

Table 1. Representation of experimental design of crossed temperature and water availability treatments.

	Ambient temperature	Warmed temperature
Variable water	AV	WV
Consistent water	AC	WC

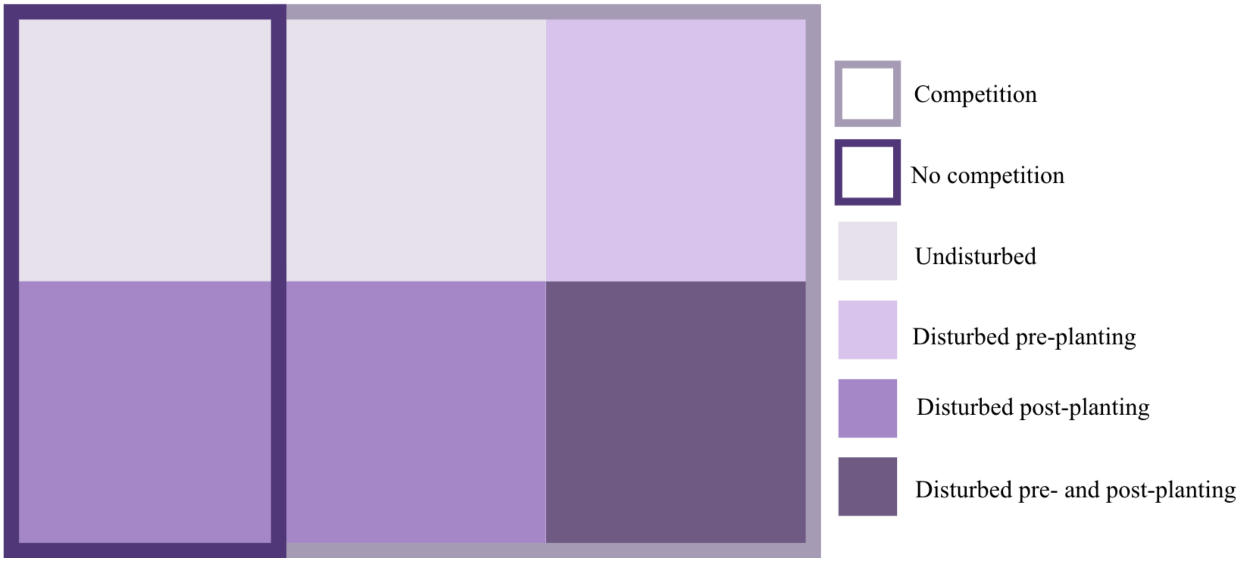

Figure 3. Representation of competition and disturbance treatments within temperature and water treatments

Pots in the warmed temperature treatment were placed on a warming mat on the benchtop, and pots in the ambient temperature treatment were placed directly on the benchtop. At the beginning of the experiment, consistent water treatments received 30 seconds of water daily from a hose nozzle designed to mimic rainfall, and the variable water treatments received 90 seconds of water every three days from the same hose. This limited only the availability of water, not the amount. Watering was reduced from the second week of the experiment to the end of the experiment to 10 and 30 second intervals due to concerns about drowning the seeds. The treatments were spatially divided for ease of identification and location of an outlet to connect the warming mats, with the warmed and ambient treatments aligned vertically across the benches and the consistent and variable water treatments aligned horizontally along the benches. Competition and disturbance treatment groups were randomly determined and distributed within each tray. Randomization within each tray maximized the independence of competition and disturbance treatments within temperature and water treatments. Trays were unable to be moved during the experiment – trays on warming mats were limited by outlet availability, and watering treatments were placed together to simplify watering and prevent splash.

In October 2024, six envelopes of *H. perforatum* seeds with a minimum of 200 seeds each were ordered from Baker Creek Heirloom seeds online catalog, and wheatgrass from the brand Magic Grow was ordered from Amazon. The first order of wheatgrass did not contain enough seeds to plant 96 pots, so a second bag from the same brand was ordered and the two bags were thoroughly mixed together during the soaking stage. 192 pots were filled to 2.5cm headspace with soaked ProMix BK25 growing medium with mycorrhizae and were left to drain excess water for approximately 24 hours. After 24 hours the tops of each pot were evened with more soaked and drained soil that had been remoistened. They were then each planted with approximately 0.7g of wheatgrass (*Triticum aestivum*) seeds, which had been soaked for 48 hours prior, and watered until saturated. The wheatgrass was then left to grow for one week. During this week, the pots were watered as needed, determined as the top 1cm of soil being dry to the touch. To maintain consistent soil conditions, this included the pots with no seeds planted.

After one week, percent coverage was estimated on the competition treatment pots by estimating how much soil was visible (i.e., not shaded out by grass). After determining percent coverage, all pots in the overlapping disturbance and competition treatment were stirred with a fork acquired from Blanchard Dining Commons, and each pot was planted with six *H. perforatum* seeds. The stirring was done by impaling the root system to the base of the fork handle nine times per pot: three times each across the top, middle, and bottom thirds of the pot, then stirring the soil for five seconds. After this process was completed on each overlapping competition and disturbance treatment pot, six *H. perforatum* seeds were planted in all 192 pots, and the warming mats were turned on to approximately 30°C.

Pots were checked for germination of *H. perforatum* seeds weekly from the date of planting. Initial germination was observed on December 3rd, 2024 and final germination data was collected on December 11th. Germination percentage was calculated by dividing the number of seeds germinated by the total number planted. After the final germination data collection, the shoots were thinned to one per pot, leaving the closest shoot to the center of each pot. The shoots in the second (post-planting) disturbance treatment were then disturbed again following the same procedure as the first disturbance. In treatments with an uneven number of germinated pots available, the greater number was left undisturbed.

Height and width measurements were taken on 12/11/2024 and 1/19/2025. Height and width measurements were taken using rulers placed against the base of each shoot, ensuring the line denoting 0 was level with the soil. The length of the plant from soil to tip was recorded as the height. The width was taken by first measuring between the two points farthest apart with the ruler held perpendicular to the edge of the bench, then parallel. Neither percent coverage nor height and width data were used in my final results owing to small sample sizes.

Due to the reduction of all pots with at least one germinated seed to only one shoot, total seed germination was used to examine treatment effects on germination and data from pots with at least one germinated seed were used when assessing survival and comparing germination and survival percentages. Data were analyzed using a chi-square calculation and by comparing percentages of germination and survival within the main water and temperature treatment groups.

RESULTS

I found the proportion of germinated seeds differed significantly across combined temperature and water treatments, but the proportion of pots with at least one germinated seed did not differ significantly across these treatments (Table 2, Figure 4, Figure 5). Temperature appeared to be less impactful than water availability (Figure 6a, 6b), including within competition and disturbance treatments (Figure 7). Variable watering appeared to reduce the number of pots with multiple germinated seeds (Figure 6b). Temperature appeared to have a less pronounced effect than water availability on germination percentage (Figure 6a). The percentage of pots with at least one germinated seed was higher than the overall germination percentage (Figure 5).

The effect of planting conditions on germination could not be reliably tested due to low replication from some treatments having nearly zero germination (Figure 7). Disturbance appears to have had a strong effect on post germination survival, but this effect was also so large that too few replicates remained for statistical analysis (Figure 8).

Table 2. Chi square values for the effects of warming and water availability treatments on *H. perforatum* germination.

	X^2	df	P value
Germination (pots)	2.56	1	>0.05
Germination (seeds)	8.48	1	<0.01

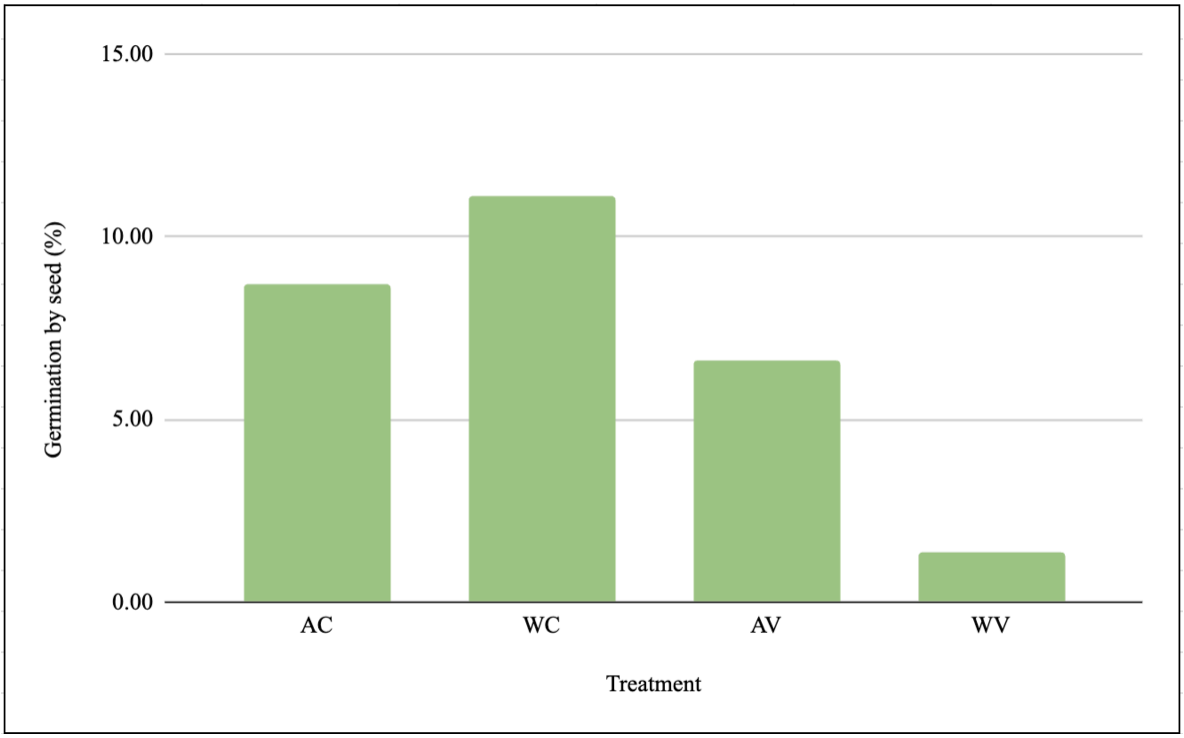

Figure 4. Total germination percentage of all planted *H. perforatum* seeds across temperature and water treatments. Treatments shown are ambient temperature/consistent water (AC), warmed temperature/consistent water (WC), ambient temperature/variable water (AV), and warmed temperature/variable water (WV).

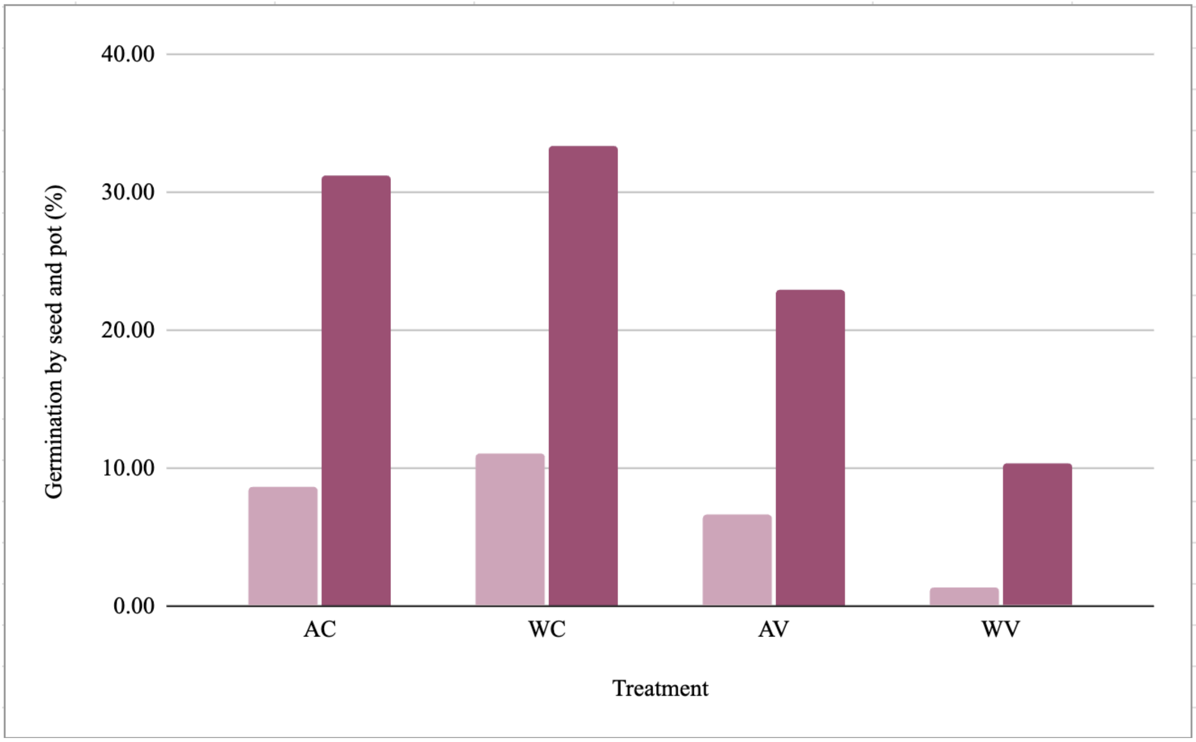

Figure 5. Germination percentages of all planted *H. perforatum* seeds (light pink) and all pots with at least one germinated *H. perforatum* seed (dark pink).

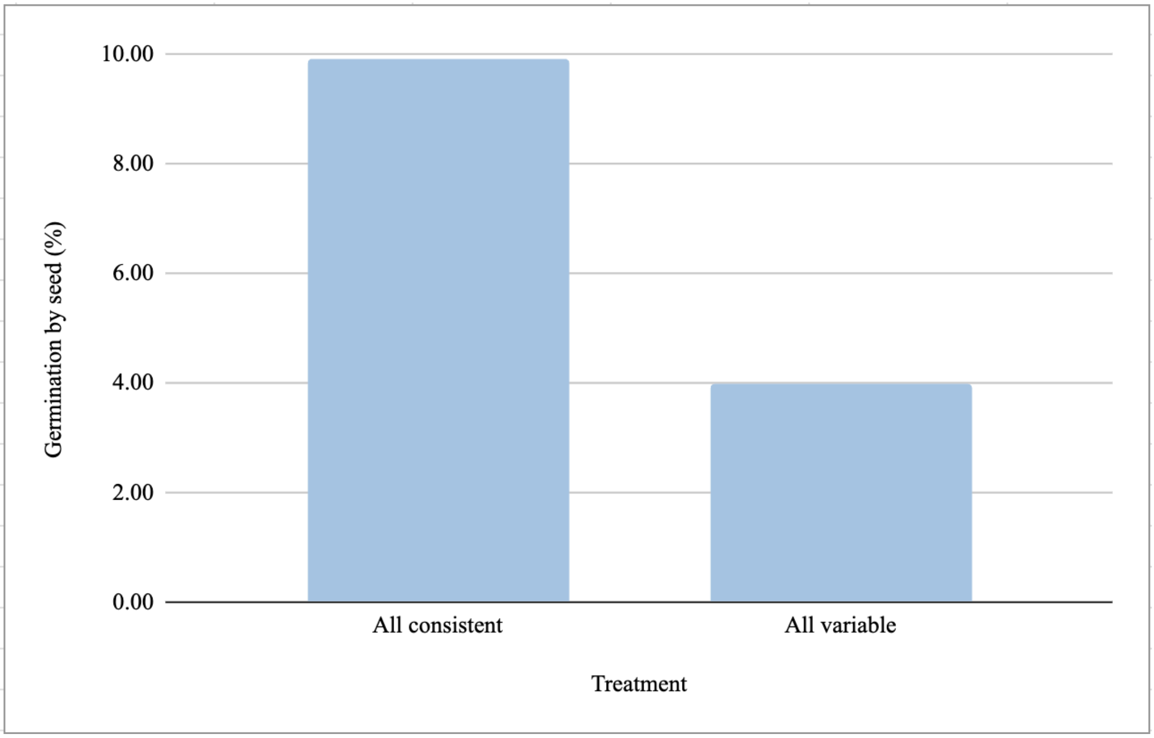

Figure 6a. Germination percentage of all planted *H. perforatum* seeds across consistent and variable watering treatments.

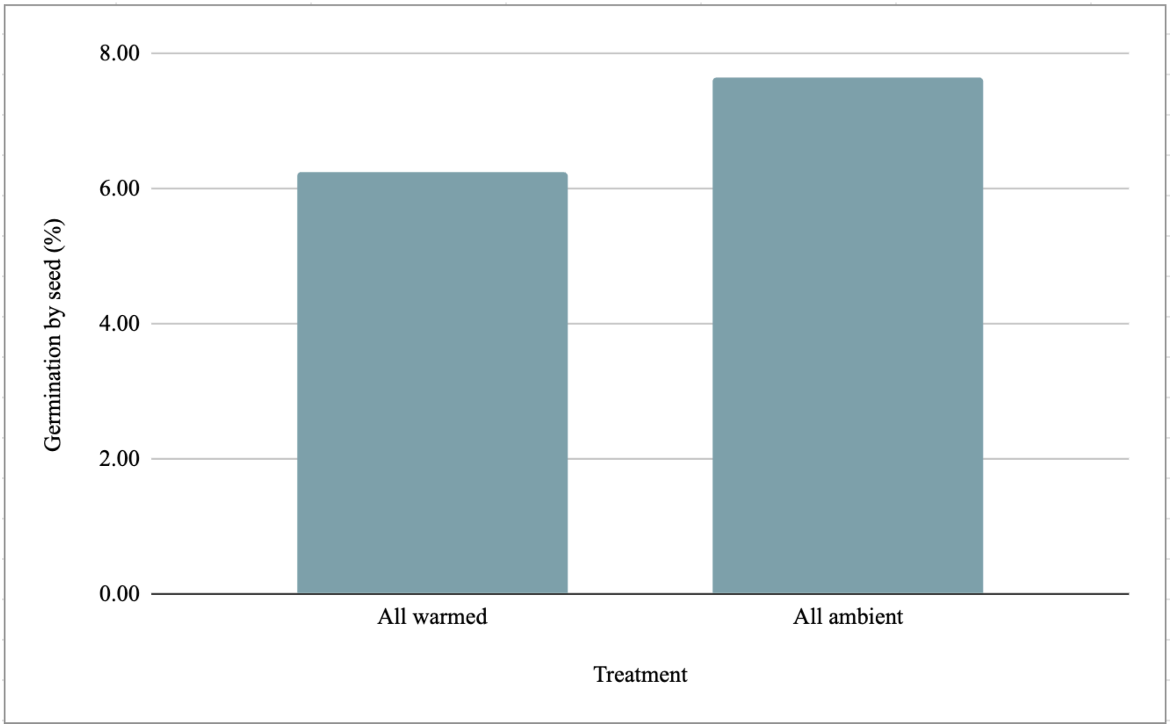

Figure 6b. Germination of all planted *H. perforatum* across warmed and ambient temperature treatments.

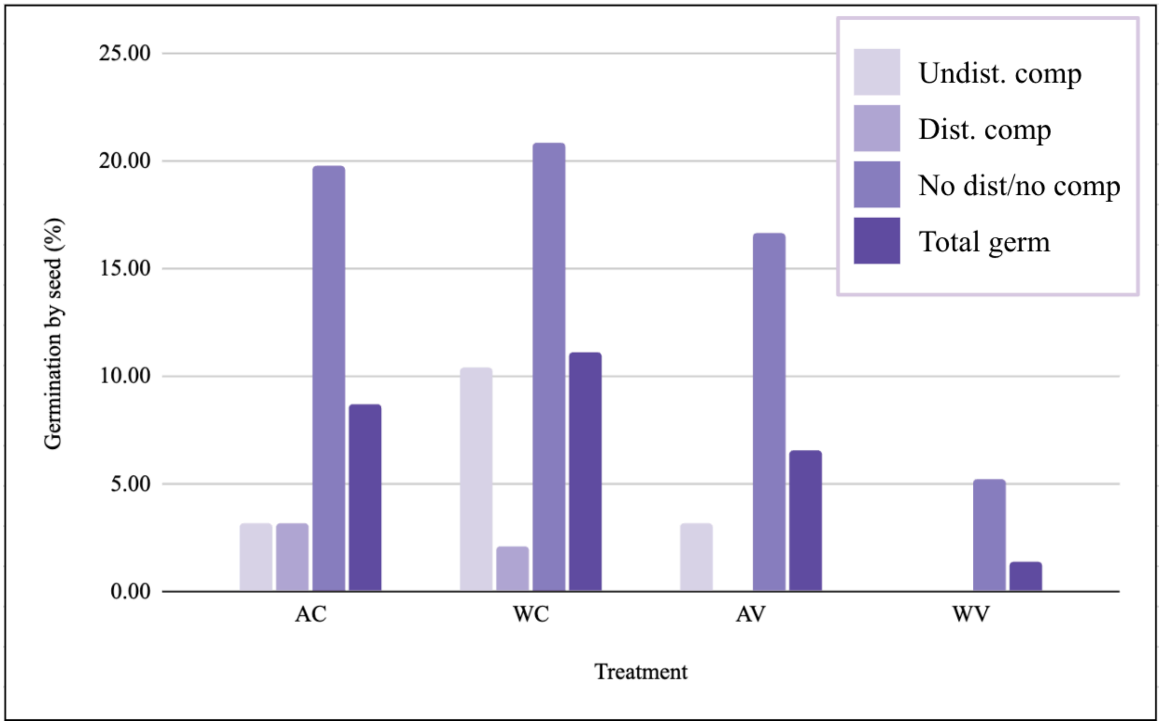

Figure 7. Total germination percentage of all planted *H. perforatum* seeds across temperature and water treatments, with competition and disturbance treatments separated. Treatments are shown left to right: pots with undisturbed competition, competition disturbed prior to *H. perforatum* planting, and no competition or disturbance, followed by the total germination percentage. Treatments shown are ambient temperature/consistent water (AC), warmed temperature/consistent water (WC), ambient temperature/variable water (AV), and warmed temperature/variable water (WV).

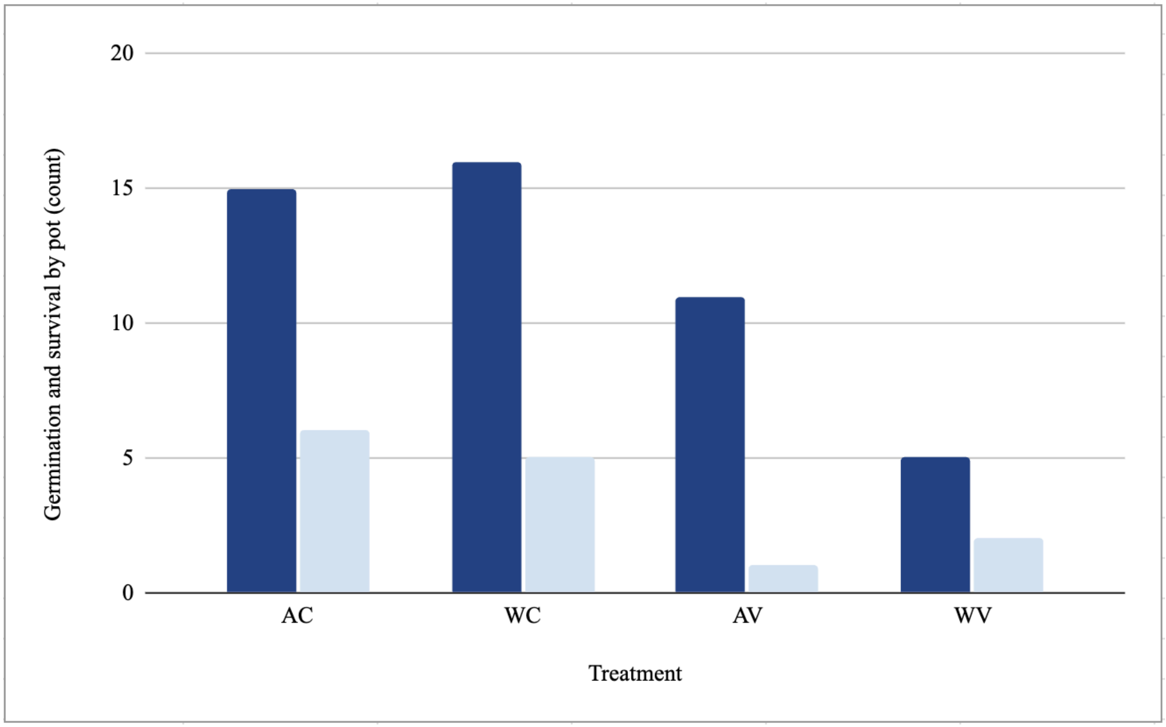

Figure 8. Count of germination (dark blue) and survival (light blue) of each pot of *H. perforatum* planted. Treatments shown are ambient temperature/consistent water (AC), warmed temperature/consistent water (WC), ambient temperature/variable water (AV), and warmed temperature/variable water (WV).

DISCUSSION

The primary goals of this research were to examine climate change factors present in New England that may have an effect on *H. perforatum* establishment and spread, and how *H. perforatum* may impact native New England species with continued climate change.

There were statistically significant differences in germination percentage between treatments involving temperature and water availability (Table 2). Germination appeared substantially impacted by temperature, the effect of which appeared highly dependent on water availability (Figure 4). Consistent water availability combined with increased temperature (WC) led to the highest germination rate, and variable water availability combined with increased temperature (WV) led to the lowest. Water availability appeared to be highly important in *H. perforatum* establishment with competition (Figure 7). Increased temperature allowed a modest increase in germination with competition when combined with consistent water, and had the opposite effect when combined with reduced water availability (Figure 7). Neither reduced water treatment had any germination in disturbed competition pots, and WV demonstrated no germination in either undisturbed or disturbed competition pots.

The percentage of pots with at least one germinated seed was far higher than the overall germination rate (Figure 6). Water availability highly impacted germination (Figure 5a), but there appeared to be little difference between warmed and ambient conditions when water availability was even between the two (Figure 5b).

Consistent water availability being essential to germination and establishment with competition was unsurprising given its previously documented importance, although its role in *H. perforatum* germination with competition appeared stronger than expected. This importance may reflect high overall resource requirements for *H. perforatum* establishment, which is compounded by the presence of competition. Previous research (Campbell, 1985; Buckley et al., 2003) demonstrates *H. perforatum's* high water requirements for both germination and survival. My results support this importance in germination (Figure 4), but have mixed results regarding survival (Figure 8).

Campbell (1985) suggested a wash to remove germination-inhibiting chemicals may be necessary for *H. perforatum* germination, which may explain the apparent importance of consistent watering during the germination stage and the possible lower importance during seedling growth post germination. However, given that all seeds across treatments received an initial watering, lack of washing is unlikely to be the case here. Humidity in the greenhouse may have blunted the effect of reduced water, or water availability simply could have become less important in the seedling stage than in the germination stage.

Water and temperature treatments show a somewhat clear trend of their effects. The effect of competition on *H. perforatum* germination is less clear. Germination in competition pots was substantially lower overall when compared to both non-competition pots and the overall germination percentage (Figure 7). Interestingly, germination was similar or lower in undisturbed competition pots than in disturbed competition pots, and disturbed competition pots had the lowest germination across the board (Figure 7). This lack of germination in disturbed competition, especially when coupled with higher rates of germination in undisturbed competition, was unexpected. The disturbance applied here may have been too intense, and so was destructive to *H. perforatum's* establishment. Undisturbed competition coupled with high resource availability has previously been shown in multiple studies (Maron & Marler, 2007; Firn et al., 2010; Vila et al., 2011; Pearson et al., 2017; Arias et al., 2023, Sun et al., 2024) to repel invasion. Across all treatments, the competition pots had extremely low survival rates (Figure 7). Non-competition pots demonstrated a substantially higher germination percentage than any competition treatment and higher survival rates (Figure 7).

Although statistical tests could not be performed on most treatments due to low replication, disturbance, both with and without competition, appeared to lead to the lowest germination and survival rates across all temperature and water treatments. Davey (1921), as cited in Harris and Gill (1997), suggested mild disturbance may facilitate *H. perforatum* establishment but highly destructive or frequently recurring disturbance was detrimental to the plant and typically led to its eradication. It is possible that the second disturbance was sufficiently destructive to destroy *H. perforatum* seedlings, rather than damage them.

Both ambient (AC) and warmed (WC) sections within the consistent watering treatment had comparable mortality percentages. *H. perforatum* seedlings in the ambient temperature and reduced water availability (AV) treatment displayed the highest percentage of post-germination mortality, while shoots in the warmed temperature and reduced water availability treatment displayed the lowest (Figure 8). Post-germination disturbance led to a mortality rate too high to examine across all temperature and water availability treatments.

Aside from the broad effect of temperature and water availability treatments, none of results discussed were able to be statistically analyzed and so cannot be considered significant. While trends may appear to be present, there is no way to definitively state the discernible effects of any treatments other than temperature and water availability.

Sources of experimental error

Low replicates with the addition of low germination rates meant the total sample size in this research was far lower than ideal. This low sample size limited my ability to examine overall trends in germination and survival and increased the possibility of confounding variables impacting my results and conclusions. The second disturbance led to extremely high mortality in surviving seedlings, which limited my ability to examine trends in survival following disturbance. Both disturbance and competition treatment survival may have been impacted by the density of the wheatgrass and the lack of open space in even disturbed wheatgrass treatments. As a result, germination and survival rates in competition treatments may not be an accurate representation of *H. perforatum's* ability to establish with competition. Overwatering in early stages of this research may have drowned some of my already limited *H. perforatum* seeds prior to germination. While overwatering may have had an effect on overall sample size, overwatering was even across treatments and was therefore unlikely to have altered treatment effects.

During the initial stages of this research, power surges and breaker resets in the greenhouse turned off the warming mats for an unknown amount of time (no greater than 12 hours) at least twice. These technical glitches may have limited the effect of warming on germination, but given the slow rate at which the warming mats cool, especially in the temperature of the greenhouse, was unlikely to have major impacts on my results. During the study period, the greenhouse suffered a cockroach infestation, which particularly affected the health of the pots in the AV treatment, which appeared to have been partially eaten by an insect. Greenhouse staff supported my theory of a cockroach being at least partially responsible for their untimely demise. The short time frame of this experiment also may have contributed to the lack of viable results – thinning of the shoots occurred shortly after sufficient germination was observed, but germination appeared to continue well into collection of survival data.

Remaining sample size during data collections was too small to be analyzed for statistical significance, and a high mortality rate contributed to the loss of most of the study population. A lack of research on *H. perforatum* presence, germination, and growth in the northeastern US also posed an issue when attempting to quantify possible factors relevant to potential future *H. perforatum* invasion in New England and the greater northeastern US. By combining my results with with literature on *H. perforatum* invasion in other regions as well as research examining similar invasive plants and invaded ecosystems, I am able to put forth several theories on *H. perforatum's* current presence and limited impact in New England and the greater northeastern US along with possible future impacts of *H. perforatum* presence as influenced climate change.

Theoretical possibilities for *H. perforatum* presence in New England and Western Massachusetts, both current and future

The enemy of my Enemy Release Hypothesis is my friend

H. perforatum's native range is also home to the beetle *Chrysolina quadrigemina,* a specialist insect predator of several varieties of *Hypericum*, including *H. perforatum.* In 1946, *C. quadrigemina* was released into California grasslands in an attempt to reduce *H. perforatum* presence there. This campaign was wildly successful, resulting in an up to 99% reduction of *H. perforatum* density in open fields (Huffaker and Kennett, 1956; van Driesche et al., 2010), and was replicated throughout the western US and some regions of western Canada (Hoebeke, 1993; van Driesche et al., 2010; Tingle et al., 2016).

Vila et al. (2005) suggest ERH to be a factor in *H. perforatum* invasion and found *H. perforatum* populations in its invasive range to have substantially higher density, lower mortality, and less insect damage than found among populations in its native range. This is further supported by the effectiveness of the biological control efforts based on introduction of *H. perforatum* predators in the western US and Canada. Successful population control as a result of the release of a native predator into *H. perforatum's* invasive range suggests that ERH is highly relevant to *H. perforatum* spread in its invasive ranges.

Following the success of *C. quadrigemina* release in the western US and Canada, a similar introduction occurred in Ontario, Canada in 1970 (Hoebeke, 1993).*C. quadrigemina* is currently present in the northeastern US and southeastern Canada (Hoebeke, 1993; Staines and Staines, 2006; Tingle et al., 2016). Although no intentional release of *C. quadrigemina* has been documented farther northeast, Fields et al. (1988) found that 18 years after its introduction to Ontario, *C. quadrigemina* had spread almost 90km (56 miles) from the site of their introduction and appeared able to locate widely geographically separated populations of *H. perforatum*, indicating the possibility of continued spread further east. Although not currently documented in New England, *C. quadrigemina* is present in New York (NY) state and some surrounding states including Pennsylvania, Maryland, and West Virginia, and has been documented there since 1989 (Hoebeke, 1993). Hoebeke (1993) also notes that several surrounding states in the northeastern US have not been surveyed to determine if *C. quadrigemina* is present.

C. quadrigemina has been shown to significantly decrease *H. perforatum* presence, in some cases completely eradicating the population (Williams, 1985; van Driesche et al., 2010). However, in ecosystems and climates dissimilar to *H. perforatum* and *C. quadrigemina's* native range, *C. quadrigemina* is significantly less effective at controlling *H. perforatum* populations (Williams, 1985). Regions in which *C. quadrigemina* introduction has been less effective have climates more similar to current and past New England. Warm, wet summers and cold winters with frost can be especially detrimental to *C. quadrigemina* mediated *H. perforatum* control (Williams, 1985; Tingle, 2016).

The current introduced range of *C. quadrigemina* in the eastern US overlaps areas of *H. perforatum's* introduced range in the northeastern US and the southern edge of *H. punctatum's* native range. This creates a region in which *H. perforatum* is in an ecosystem and climate dissimilar from its native range, but no longer freed from one of its native predators. *C. quadrigemina* is also a novel predator to native *H. punctatum*, which lacks the toxic defenses of *H. perforatum* and may be wholly unable to defend itself against *C. quadrigemina* (CITE USDA). Specialist predators such as *C. quadrigemina* are frequently able to consume congeners of their host species, and may even prefer to do so if their host species has evolved specialized defenses (Agrawal & Kotanen, 2003).

Despite its original purpose of reducing *H. perforatum* populations, the introduction of *C. quadrigemina* may be unwittingly backfiring and increasing *H. perforatum* populations in the eastern US. Consumption of *H. punctatum* by *C. quadrigemina* could be a factor in decreasing *H. punctatum* populations in the eastern US, which could in turn lead to the opening of a niche highly likely to be suitable for *H. perforatum*. Tingle et al. (2016) recorded *C. quadrigemina* in central NY state consuming both *H. perforatum* and *H. punctatum*. In a field study, the same researchers found that *C. quadrigemina* preferred to consume *H. punctatum* over *H. perforatum* and significantly reduced *H. punctatum* populations in fields, grasslands, and clearings (Tingle et al., 2016). They did not examine if *H. punctatum* decline due to the introduction of the novel predator had any significant impact on local *H. perforatum* populations. However, it is possible that the impact of predatory removal would be much greater on *H. punctatum* populations than *H. perforatum* due to *H. perforatum's* ability to colonize an area substantially more rapidly than *H. punctatum*.

While current northeastern US climate is less than ideal for *C. quadrigemina*, climate change may be making it more favorable. The precipitation and temperature shifts affecting New England are also having significant impacts on water availability and soil moisture in other northeastern US regions, including regions of central NY state with a documented *C. quadrigemina* presence (Tingle et al., 2016; Hess et al., 2024). *C. quadrigemina's* northeastern US range currently does not extend beyond states bordering New England, but, as temperatures and precipitation variability in the northeastern US continue to increase, *C. quadrigemina's* habitable range may expand northward and possibly into New England due to increasing overlap of climate conditions in the northeastern US and *C. quadrigemina's* native mediterranean climate.

If temperature and precipitation variability increase to the point of massively reducing the habitable range of *H. punctatum* or other grassland natives, and *H. perforatum* is able to effectively utilize the open niche space, *H. perforatum* populations in the northeastern US could increase sufficiently to render *C. quadrigemina* biocontrol effective. This possibility remains unlikely as large-scale climate and habitat factors still appear to limit *H. perforatum* spread in the northeast and New England, but with appears possible with sufficient disturbance and deforestation when combined with climate change. *C. quadrigemina* biocontrol may also become effective in the northeast if *H. punctatum* populations are sufficiently reduced via *C. quadrigemina* predation that *H. perforatum* becomes the only or most widely available food source. Given *C. quadrigemina's* documented difficulty in establishing in wet and cold regions, this is less likely without at least some significant warming and drying impact of climate change.

Increasing heat and precipitation variability together will not permit sufficient germination

Observations by Clark (1953) indicate *H. perforatum* in its invasive range has high water requirements for germination, which is supported by Harris (1951) and Buckley (2003) who found *H. perforatum* to establish in its invasive range in Australia only with more than 76 cm of yearly rainfall, and in its invasive range n the US in regions with more than 89 cm of yearly rainfall. *H. perforatum* also has been noted to require fewer total inches of precipitation in the form of snow as opposed to rain (Harris, 1951).

Supporting these observations, WV had the lowest germination percentage of all temperature and water treatments (Figure 3), indicating a lack of consistent water availability to be detrimental to *H. perforatum* germination when combined with increased temperature. Observations by Campbell (1985) indicate *H. perforatum* has significantly reduced germination without a water wash to remove germination-inhibiting chemicals on the seed, further suggesting water availability to play a pivotal role in *H. perforatum* germination.

H. perforatum is also dependent on warmth for germination (Zouhar, 2004; Nunes et al., 2019). Nunes et al. (2019) found *H. perforatum* seeds to have the highest germination rate within their study at 25°C, which is similar to current New England summer temperatures. Temperatures both above and below 25°C appeared to have detrimental effects on germination rate, with a higher temperature of 30°C leading to substantially lower germination (Nunes et al., 2019). Clark (1953) noted that temperatures greater than 27°C reduced *H. perforatum* germination, which was supported by Campbell (1985) in his examination of factors affecting *H. perforatum* germination. Campbell (1985) found temperatures greater than 27°C to have strong inhibitory effects on germination. These findings indicate a temperature ceiling of approximately

27-30°C past which warmth may inhibit *H. perforatum* germination. However, this may be less applicable to populations locally adapted to New England, as seasons with the warmest temperatures also tend to have the highest rainfall (Young & Young, 2021; Miller, 2025). *H. perforatum* in its invasive range in New Zealand germinates in cooler temperatures than in its native range, suggesting population-specific adaptation to germinate under wetter conditions (Beckmann et al., 2011).

My results in WV and WC treatments support the idea that water availability may alter the temperature range in which *H. perforatum* is able to germinate. The WC treatment had the highest overall germination rate, despite being outside the optimal range for *H. perforatum* germination (Figure 4). It is possible that the addition of daily water in the WC treatment kept the soil at a lower temperature closer to *H. perforatum's* optimal germination range, or that consistent water availability reduced the inhibitory effects of increased temperature. Data from Clark (1953) and Campbell (1985) also indicate that water availability may significantly affect the regions in which *H. perforatum* can successfully establish. Increased temperature combined with high water availability appears to substantially increase *H. perforatum's* germination rate, which could have significant effects on its ability to colonize areas of New England. Since the effect of warmer temperatures appears dependent on water availability, *H. perforatum's* future impacts will likely be heavily impacted by precipitation patterns.

Both water availability and temperature in New England have fluctuated in recent decades (Rustad et al., 2011; Beylen and Jain, 2015; Karmalkar and Bradley, 2017; Young and Young, 2021; Miller, 2025). New England is warming at a faster rate than many other areas of the globe, with a more rapid rate of increase predicted to continue (Rustad et al., 2011; Karmalkar & Bradley, 2017; Young & Young, 2021; Miller, 2025). New England climate has shifted to have shorter, warmer winters (Beylen & Jain, 2015; Young & Young, 2021) and hotter summers (Descamps et al., 2021; Young & Young, 2021; Miller, 2025), with the summer of 2024 having the highest temperatures recorded in New England to date (Miller, 2025). Minimum temperatures have increased more than maximum temperatures, leading to reduced snowfall in the winters, earlier spring icemelt (Beylen & Jain, 2015), and longer periods of sustained high temperatures in spring, summer, and fall months (Betts, 2011; Young & Young, 2021). Precipitation frequency is decreasing (Young & Young, 2021) while total precipitation increases (Karmalkar & Bradley, 2017; Miller, 2025).

The predicted changes in temperature and precipitation frequency will both likely lead to a reduction in soil moisture: earlier and faster snowmelt will lead to more rapid spring flooding, the pace of which the soil will be unable to adequately absorb (Beyen & Jain, 2015; Young & Young, 2021), and less frequent rainfall with hotter temperatures between precipitation events has been shown to cause greater evaporation from the soil (Young & Young, 2021; Miller, 2025). This will also increase the risk of flooding in the summer months as the soil will be less able to absorb the high amounts of infrequent precipitation (Young & Young, 2021).

Higher overall precipitation at less frequent intervals could lead to increased fire risk and die-offs of native species and pollinators (Crausbay, 2017; Descamps et al, 2021). This change may be pronounced in temperate climate regions such as New England temperate forests due to the ecosystem dependence on consistent rainfall during spring and summer months (Descamps et al., 2021), and could have substantial effects on *H. perforatum* germination during those months due to its demonstrated dependence on consistent rainfall (Clark, 1953). The above climate and weather changes move possible future New England climate closer to the climate in *H. perforatum's* native range, which may favor *H. perforatum* over native species and lead to increased invasion risk even if warmer temperatures do not continue to coincide with increased water availability.

The above climate and weather changes move possible future New England climate closer to the climate in *H. perforatum's* native range, which may favor *H. perforatum* over native species and lead to increased invasion risk even if

warmer temperatures do not continue to coincide with increased water availability. Current *H. perforatum* populations may not be able to take full advantage of this shift if local adaptation to New England climates has occurred, although relevant genes may remain even in locally adapted populations.

Continuing native species decline as a result of the above factors may lead to die-offs, and ecosystem disturbance may also open niches in which *H. perforatum* may be able to establish. A reduction in native diversity or forest cover will likely decrease biotic resistance in ecosystems currently resistant to *H. perforatum* invasion, which could also provide avenues through which *H. perforatum* could establish. However, even with said impacts, resource availability would likely be insufficient to allow *H. perforatum* to outcompete neighboring native species, especially under conditions unfavorable to both (Pearson et al., 2017). Even when accounting for possible native decline and lower ecosystem resistance as a result of climate change, projected future climate for New England does not appear to be sufficiently favorable to allow widespread *H. perforatum* invasion from current populations.

Although climate change may lead to reduced invasion risk from the current *H. perforatum* populations in New England, a newly introduced population may have different results. A common trait in many invasive species is population level or local adaption (Coates, 2008; Willis et al., 2010; Beckmann et al., 2011; Clements and Jones, 2021). This allows many invasives to more closely align with climate conditions and habitable niche space in their introduced ranges, and may help outcompete native species by altering timing of germination and flowering to occur at a more favorable timing (Willis et al., 2010). *H. perforatum* has demonstrated local adaptation in both its invasive (Beckmann et al., 2011) and non-native (Coates, 2008) ranges, which is likely increasing its competitive ability, especially with effects of climate change increasing globally. *H. perforatum* in the northeastern US, including New England, has demonstrated adaptation to annual weather patterns and typical seasonal climates (Coates, 2008). This adaptation currently likely increases the fitness of *H. perforatum* populations in New England, but may prove detrimental with continued climate change impacts. *H. perforatum* in the US and much of its invasive range has demonstrated high water availability requirements, and does not appear to handle drought conditions well, especially when combined with high temperatures (Clark, 1953; Campbell, 1985).

As climate change continues to increase temperatures and water variability in New England, current locally adapted populations of *H. perforatum* are not likely to become invasive. However, a reintroduction of *H. perforatum* from its native range may be. *H. perforatum's* native range is highly similar to projected future New England climate with continued climate change, with hot, dry summers and cool rainy winters. Similar climates in the northwestern US, southwestern Canada, Australia, and New Zealand have proven highly susceptible to *H. perforatum* invasion (Campbell, 1985; Zouhar, 2004; Groenteman et al., 2011). An introduction of non-locally adapted *H. perforatum* combined with a continued shift of New England climate towards one more similar to *H. perforatum's* native range may significantly alter its invasion capability, and lead to widespread *H. perforatum* invasion in New England. However, given the importance of non-climate factors in controlling *H. perforatum* invasion, even a population perfectly fit for the projected climate would likely struggle to invade New England.

Although there are several possible avenues through which future climate change could alter *H. perforatum* presence in New England, climate change has already altered New England ecosystems and *H. perforatum* has demonstrated an ability to respond to climate stressors currently present. Given this, current climate change effects appear to be an insufficient explanation for the current lack of *H. perforatum* presence. Factors other than climate alone are a more likely explanation for the current lack of *H. perforatum* presence, and may continue to play a greater role than climate factors in limiting possible future invasions.

Biotic resistance may be weakened or strengthened by climate change

The presence of previously established native species (Firn et al., 2010; Yanelli et al., 2017; Yanelli et al., 2020) and high biodiversity (Hector et al., 2001;

Gelbard & Harrison, 2005; Oakley et al., 2013; Haeuser et al., 2018; Cheng et al., 2024) may significantly increase invasion resistance of an ecosystem. Climate change and disturbance may increase invasion risk by reducing native populations, leading to reduced biodiversity and biotic resistance (Schuster et al., 2020; Lanta et al., 2022; Sun et al., 2024), and may create more favorable conditions for invasive species to establish (Firn et al., 2010; Liu, 2016; Haeuser et al., 2017; Haeuser et al., 2018; Sun et al., 2024). Rapid invasion is significantly more likely to occur following disturbance or loss of biodiversity (Haeuser et al., 2017; Haeuser et al., 2018; Cheng et al., 2024; Sun et al., 2024), which both occur when native species undergo climate change mediated mass die-offs. Native species functionally similar to would-be invaders likely also play a role in resisting invasion (Gilbert & Lechowicz, 2005; Firn et al., 2010; Yanelli et al., 2017), but appear to be less important than overall well-established native populations (Firn et al., 2010; Yanelli et al., 2017; Yanelli et al., 2020).

As both a functionally similar and well established native species, *H. punctatum* may be a factor in reducing *H. perforatum* invasion risk in New England. As *H. punctatum's* habitable niche continues to be altered by both biotic and abiotic effects, climate change may become an increasingly important factor in *H. punctatum* interactions with *H. perforatum.* Given the functional and morphological similarities between *H. perforatum* and *H. punctatum,* habitats favorable for *H. punctatum* growth are also likely to be favorable for *H.*

perforatum growth. Thus, previous *H. punctatum* establishment may prevent *H. perforatum* from fully taking over a suitable niche, limiting possible further expansion. Climate change may alter *H. punctatum's* current niche, the ability of *H. punctatum* or *H. perforatum* to germinate and grow, *H. perforatum's* ability to establish in *H. punctatum's* niche, as well as some combination or none at all of the previous factors.

There is limited data on current *H. punctatum* presence in New England, as well as on possible interactions between *H. punctatum* and *H. perforatum.* Coates (2008) visited six sites with five 2x2m plots in each around the Quabbin Reservoir and found *H. perforatum* present in the vegetation of 23 plots and in the seed bank in 16 plots, but overlapping in only 7 plots. *H. punctatum* was not present in the seed bank in any plots, nor in the vegetation where *H. perforatum* was present, indicating *H. perforatum* may be replacing *H. punctatum* in some area of New England. It is somewhat unclear if *H. perforatum* is taking over spaces previously occupied by *H. punctatum*, arriving and establishing first in spaces *H. punctatum* would have been able to occupy, or establishing in a completely different niche and is not affecting *H. punctatum* populations whatsoever. *H. perforatum* presence having zero impact on *H. punctatum* populations is highly unlikely, given the high morphological similarities and overlap of niche space between the two.

H. perforatum may have a competitive advantage over *H. punctatum* when considering the effects of climate change in New England. *H. punctatum* is likely less able to adapt to the rapidly increasing temperatures and water variability than *H. perforatum*, which displays high levels of plasticity (Maron et al., 2004; Zouhar, 2004; Dlugosch et al., 2015) and local adaptation (Beckmann et al., 2011), including in New England populations (Coates, 2008). Both high plasticity and rapid population level adaptation may allow *H. perforatum* to outcompete native species, especially if native species are struggling to adapt to climate change factors altering their habitable niche (Maron et al., 2004; Zouhar, 2004; Beckmann et al., 2011; Dlugosch et al., 2015). Increasing temperatures and precipitation variability may be facilitating this possible replacement by reducing or altering *H. punctatum's* niche to make it less favorable, allowing *H. perforatum* to outcompete *H. punctatum.* In addition, as climate condition shift toward a range more similar to *H. perforatum's* native range, its performance may improve even more relative to *H. punctatum* even with local adaption. This increased competitive ability may allow *H. perforatum* to overtake spaces formerly occupied by *H. punctatum* when given appropriate opportunity.

Interactions between *H. perforatum* and *H. punctatum* may be relevant for local biodiversity and native species distribution, but relatively unimportant to overall *H. perforatum* presence in New England. *H. perforatum* appears to be outcompeting *H. punctatum* in many New England regions, but interactions between *H. punctatum* and *H. perforatum* may be less relevant to both invasion resistance and *H. perforatum* presence in New England than previously thought. The most likely explanation for *H. perforatum* replacement of *H. punctatum* presence is H. punctatum is simply being outcompeted by *H. perforatum*, and the resulting reduction in *H. punctatum* population is not highly affected by climate change nor having any significant impact on *H. perforatum* invasion in New England. While reductions in overall biodiversity would likely have a significant impact on *H. perforatum* invasion, *H. punctatum* is just one piece of the ecosystem and alone is unlikely to have any major effect on *H. perforatum* invasion risk.

Although *H. punctatum* alone likely does not have any significant effect on *H. perforatum* invasion in New England, the threats climate change poses to *H. punctatum* also apply to many other components of the wider ecosystem, which is far more important than any single species when examining invasion resistance. Native plants often struggle to adapt to long-term ecosystem changes, especially when compared with similar invasive populations (Willis et al., 2010; Merow et al., 2017). This means that climate change often has greater effects on native populations, which can open niches for invasives to spread after establishing in the area (Alpert et al., 2000; Firn et al., 2010; Willis et al., 2010; Merow et al., 2017; Xavier et al., 2017; Sun et al., 2024).

Climate change is often more detrimental to native species than previously established and already present invasives (Liu, 2016; Haeuser, 2017; Haeuser, 2018) but can also aid in repelling invasion in previously uninvaded ecosystems (Pearson et al., 2017; Cheng et al., 2024). The differing impacts may lead to a varying effect of climate change on invasive species: invasives already present in an ecosystem could increase in population, while invasives recently introduced to an ecosystem may be unable to establish and invade. *H. perforatum* is well-established in New England (Coates, 2008), and as such may be more positively affected by climate change than an invasive population attempting to establish, but may also not have sufficient invasion potential in New England ecosystems to establish a truly invasive population.

Non-climate factors increasing *H. perforatum* invasiveness in the western US such as rapid local adaptation and plasticity may be relevant to continued *H. perforatum* presence in New England, but do not appear to be sufficient to permit invasion. New England temperate forests are not an ideal invasive range for *H. perforatum*, which is notably a grassland invader (Zouhar, 2004) that thrives in open spaces with full sun and low competition. This may simply not be an ecosystem invadable by *H. perforatum* without massive ecosystem disruption substantially reducing forest cover or otherwise increasing the amount of disturbed open areas with low competition.

A combination of ecosystem composition, biotic resistance, and land use history, rather than climate factors, limit H. perforatum invasion in New England

Allen and Bradley (2016) suggest that non-climate factors may be limiting invasion in the northeastern US, noting that projected species richness as a result of invasion is lower than actual species richness in most regions of the northeast. Their findings suggest many invasive species would be able to populate a region or ecosystem if climate conditions were solely responsible for survival and establishment, but that so far fewer invasive species than predicted by climate modeling have established in the northeastern US and New England. Their findings appear to be supported in the case of *H. perforatum* presence in New England: despite currently favorable climate conditions, *H. perforatum* remains non-invasive in New England. As a result, non-climate factors may be playing a greater role in permitting or inhibiting *H. perforatum* establishment than climate change. Possible non-climate factors include ecosystem composition, native populations, predation, current human and animal activity, and land use history in invaded and resistant regions. History of *H. perforatum* invasion may also support climate factors having a limited effect on invasiveness. *H. perforatum* was already highly invasive in Australia in the late 19th century (Harris & Gill, 1997), well before documented climate change was a major driver of invasion.

H. perforatum's native range falls largely within regions of Europe, West Asia, and Northern Africa (Zouhar, 2004). Its invasive range lies mostly within the same latitudes in the western US and Canada, as well as in mirroring latitudes of southern temperate forest regions in Australia and New Zealand (Zouhar, 2004; Beckmann et al., 2011; Morrison et al., 2017). *H. perforatum's* native range is largely within a Mediterranean climate with hot, dry summers and cool, rainy winters (Zouhar, 2004), and much of its invasive range across the US, Australia, and New Zealand has similarly patterned climate conditions, with distinct dry and rainy seasons (Zouhar, 2004). Snow does not appear detrimental to *H. perforatum* establishment (Harris, 1951). Although New England climate is not overly similar to *H. perforatum's* native or invasive ranges, Walker et al. (2001) noted *H. perforatum* to establish well in disturbed areas within temperate climates in its introduced ranges, implying climate conditions are viable for *H. perforatum* to maintain a self-sustaining population throughout the New England.

While climate conditions between *H. perforatum's* native and invasive ranges are similar, ecosystem composition is not. *H. perforatum* is mainly native to shrubland and grassland; regions in the Western US, Australia, and New Zealand where *H. perforatum* is classified as an invasive are nearly all grassland, rangeland, or pasture either previous or current (Zouhar, 2004), and New England is dominated by forest (Foster, 1992; Rustad et al., 2011) with limited natural grassland. Although *H. perforatum* is able to establish in all three ecosystems, it is only invasive in grassland, rangeland, and pasture. This suggests *H. perforatum's* invasion capability to be highest in grassland, especially disturbed grassland, and limited in ecosystems with higher woody biomass. Dunwiddie et al. (1996) support this conclusion, having noted *H. perforatum* to be less present in shrublands in the US, and also show *H. perforatum* to have higher occurrence in fields dominated by other non-native species, supporting a difficulty in establishing in areas with high biodiversity or previously uninvaded areas. *H. perforatum* has demonstrated difficulty establishing with competition, in particular undisturbed competition (Sampson & Parker, 1930; Tisdale et al., 1959; Campbell, 1985). *H. perforatum's* niche in shrubland may simply be already filled by a native competitor with which *H. perforatum* is unable to compete, leaving *H. perforatum* unable to establish. Firn (2010) and Yanelli et al. (2017) found established native community to resist invasion, but invasives to outcompete natives when sown together, demonstrating established ecosystems' strong resistance to invasion.

Even forest clearings lack the low competition, full sun habitat in which *H. perforatum* appears most highly invasive. *H. perforatum's* presence in New England also appears somewhat limited to regions less heavily wooded and with more cleared and disturbed land (Foster, 1992; Coates, 2008), further suggesting grassland to be more easily invadable by *H. perforatum.* Taken with the above observations by Dunwiddie et al. (1996), a possible conclusion for *H. perforatum's* lack of dominance in New England is that *H. perforatum* is only invasive in grassland, and not in the high forest coverage regions of New England. However, both ecosystem composition and climate may be less important in resisting *H. perforatum* invasion than human and livestock activity. Although *H. perforatum* is notably invasive in grassland, in much of its invasive range, *H. perforatum* establishes almost exclusively with prior disturbance (Zouhar, 2004), which is highly dependent on land use.

In addition to differing community composition, land use in New England is vastly different from the western US (Foster, 1992; Gilliam, 2016). Main New England industries have historically included logging and cropping (Foster, 1992), which may facilitate initial *H. perforatum* germination as the land is cleared (Del Tredici, 1977; Zouhar, 2004), but may then destroy seedlings as a result of consistent and high disturbance levels (Davey, 1921 via Harris & Gill, 1997). Clearcutting, however, may highly facilitate *H. perforatum* germination by creating the full sun, low competition habitat preferred by *H. perforatum* (Del Tredici, 1977). In addition, New England nearly completely lacks the widespread grassland of the western US, and much of the grassland and rangeland in *H. perforatum's* invasive range is pasture (Zouhar, 2004) which undergoes regular disturbances such as grazing that frequently reduce native biomass and may increase invasion risk especially at higher levels (Xiang et al., 2021; Wu et al., 2023; Cao et al., 2024). While agricultural land is present in New England, much of the land designated for agricultural use is cropland, not pasture (Foster, 1992). This difference likely plays a role in the lack of *H. perforatum* invasion throughout New England.

Cropland has high, regular disturbance specifically designed to discourage the growth of weeds and other invasive or pest species, and to facilitate the growth of the planted crop, making it a less than ideal environment for invasive species establishment. Pasture has consistently high disturbance levels from grazing, which typically facilitates, rather than inhibits, invasive establishment by damaging and removing native species, opening spaces for invasive species to grow and spread (Xiang et al., 2021). Pasture is also not intentionally sown like cropland is, which leads to the open spaces being colonized by the first species able to establish and sustain a population rather than having growth of a specific crop supported. Maron et al. (2004) note that *H. perforatum* in the central US states was likely prevented from reaching the same prevalence as in central-western US states due to the main land use of the region being for cropping rather than pasture.

The role of pastureland specifically in *H. perforatum* invasion risk is further supported by Grant (1990), Tisdale (1976), and Bunting et al. (2002), who note *H. perforatum* presence to be highest in areas overgrazed in in the early 20th century, that at the time of invasion were no longer composed of native grasses. In some areas the grass population was largely composed of annual species, which *H. perforatum* was able to easily outcompete by simply outliving them (Tisdale, 1976). Later work by Wu et al. (2023) and Cao et al. (2024) also suggest that damage as a result of overgrazing can lead to increased invasion risk and establishment of invasive species due to a reduction in native biomass and biodiversity. Species turnover is much higher in grazed pasture and grasslands (Xiang et al., 2021; Wu et al., 2023; Cao et al., 2024), which leads to more frequent open niches. Grazing can also contribute to high species replacement (Sanaei et al., 2018), which also can contribute to invasive species presence. When open niches are present, invasive species are far more equipped to establish themselves and crowd out natives before they are able to re-establish themselves in a disturbed area (Alpert et al., 2000; James and Drenovsky, 2007; Betekhtina et al., 2019).

Northern forests appear to be highly resistant to *H. perforatum* invasion, leading to limited biological impact of *H. perforatum* presence. However, *H. perforatum* establishment as a result of seed bank germination has been documented in forests following clear-cutting or other disturbance leading to the removal of competition (Zouhar, 2004). This suggests high forest coverage in New England to play a significant role in regulating *H. perforatum* presence and increasing invasion resistance. Schuster (2020) and Lanta (2022) both note forest ecosystems to be highly resistant to invasion by a variety of species, with resistance being reduced greatly by human disturbance. Post-disturbance establishment is a common feature of *H. perforatum* invasion (Sampson & Parker, 1930; Tisdale et al., 1959; Parendes and Jones, 2000), as well as establishment in areas with limited competition (Campbell, 1985). Coates (2008) found *H.*

perforatum to have a high seed bank presence in New England. With reduced forest coverage, *H. perforatum* could become substantially more prevalent, depending on the affected region and land use post-deforestation. However, even with an increased presence in non-forested areas, H. *perforatum* populations would still likely be unable to spread as rapidly and cause such widespread disruption as in the western US. Despite recent increases in deforestation, total forest coverage in New England remains high, and pasture land use low (Foster, 1992; Bahlai et al., 2021), substantially limiting *H. perforatum's* invasion potential in New England.

Heavy forest combined with much open land lacking the disturbance patterns most favorable to *H. perforatum* establishment explains much of the lack of current invasion in New England. A combination of land use both historical and current and ecosystem composition appear to the greatest predictors of current vulnerability to *H. perforatum* invasion. Climate change may continue to play a role, largely through altering ecosystem composition of grasslands, but appears to have a currently limited effect on *H. perforatum* establishment throughout both its non-native and invasive ranges. While this research focuses on the factors affecting *H. perforatum* presence within New England, the trend of *H. perforatum* establishing a considerable presence but remaining non-invasive is similar across other regions of the northeast (Morrison et al., 2017) Similarly to

New England, Morrison et al. (2017) note large populations to be present in eastern Canada, but not causing widespread ecosystem or habitat damage.

Without the highly invadable pasture and grassland, *H. perforatum* is severely limited in its ability to establish and expand in much of northeastern North America, including New England. Even as climate change continues to alter New England's ecosystems and weather, it is unlikely to lead to conditions that would alter the landscape to the extent where *H. perforatum* invasion would be possible to the extent in the western US. Climate change altering New England climate and ecosystems in such a way as to increase vulnerability to *H. perforatum* invasion is possible, but the climate specific factors both currently having and predicted to have the greatest effect on New England will likely have little effect on *H. perforatum's* invasion capability. The more likely culprits for an increase in *H. perforatum* presence would be factors such as disturbance and deforestation that directly lead to open niches, and even those would be unlikely to have have any significant effect on the ability of *H. perforatum* to become widespread or invasive throughout New England.

Conclusions

H. perforatum presence in New England is regulated by a myriad of climate and non-climate factors, with large scale (ecosystem determining) climate and non-climate factors appearing to have the greatest importance in preventing invasion. Forest cover appears to have a greater impact than climate in terms of limiting *H. perforatum* population spread, although that could shift with increased effects of climate change altering native species niches or otherwise leading to shifts in native populations and forest cover. Despite possible niche takeover by *H. perforatum*, interaction between *H. perforatum* and *H. punctatum* likely does not play a major role in preventing *H. perforatum* invasion in New England.

Locally adapted populations of *H. perforatum* may struggle to germinate with increasing effects of climate change, but will likely still outcompete the native *H. punctatum*. A population of *H. perforatum* newly introduced from its native range could possibly be more invasive in New England's projected future climate than current locally adapted populations, but would be unlikely to be able to establish well. Biotic resistance and an unsuitable ecosystem would likely still majorly reduce *H. perforatum* invasion risk even with a population well-suited to the climate. Disturbance leading to seed bank germination of currently dormant *H. perforatum* could also impact total population, but would be unlikely to lead to *H. perforatum* invasion in New England.

Climate change in New England appears unlikely to play a major role in affecting *H. perforatum's* invasion capabilities in the region. ERH may apply to *H. perforatum* populations in New England, but does not appear to have an impact on invasiveness in the region, and certainly not to the extent apparent in the western US, Australia, and New Zealand. Current factors limiting *H. perforatum* establishment in New England are likely centered around past and current land use and currently established populations of native species, including high forest coverage, and are only minimally influenced by climate change.

LITERATURE CITED

Abbass, K., Qasim, M.Z., Song, H., Murshed, M., Mahmood, H., & Younis, I. (2022). A review of the global climate change impacts, adaptation, and sustainable mitigation measures. *Environmental Science and Pollution Research, 29*, 42539-42559. https://doi.org/10.1007/s11356-022-19718-6

Agrawal, A.A. & Kotanen, P.M. (2003). Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters, 6*, 712-715. https://doi.org/10.1046/j.1461-0248.2003.00498.x

Allen, J. M., & Bradley, B. A. (2016). Out of the weeds? Reduced plant invasion risk with climate change in the continental United States. *Biological Conservation, 203*, 306–312. https://doi.org/10.1016/j.biocon.2016.09.015

Alpert, P., Bone, E., & Holzapfel, C. (2000). Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics, 3*(1), 52–66. https://doi.org/10.1078/1433-8319-00004

Antão, L.H., Weigel, B., Strona, G., Hällfors, M., Kaarlejärvi, E., Dallas, T., Opedal, O.H., Heliölä, J., Henttonen, H., Huitu, H., Korpimäki, E., Kuussaari, M., Lehikoinen, A., Leinonen, R., Lindén, A., Merilä, P., Pietiäinen, H., Pöyry, J., Salemaa, M., Tonteri, T., Vuorio, K., Ovaskainen, O., Saastamoinen, M., Vanhatalo, J., Roslin, T., & Lain, A. (2022). Climate change reshuffles northern species within their niches. Nature Climate Change, 12, 587-592. https://doi.org/10.1038/s41558-022-01381-x

Arias, G., Zeballos, S.R., & Ferreras, A.E. (2023). Competition effect exerted by two nonnative invasive plant species on a native under contrasting conditions of resource availability. *Biological Invasions, 25*(7), 2261-2276. https://doi.org/10.1007/s10530-023-03039-x

Bahlai, C. A., Hart, C., Kavanaugh, M. T., White, J. D., Ruess, R. W., Brinkman, T. J., Ducklow, H. W., Foster, D. R., Fraser, W. R., Genet, H., Groffman, P. M., Hamilton, S. K., Johnstone, J. F., Kielland, K., Landis, D. A., Mack, M.C., Sarnelle, O., & Thompson, J. R. (2021). Cascading effects: insights from the U.S. Long Term Ecological Research Network. *Ecosphere, 12*(5). doi: 10.1002/ecs2.3430

Barros, V., Melo, A., Santos, M., Nogueira, L., Frosi, G., & Mauro Guida Santos, G.M. (2020). Different resource-use strategies of invasive and native woody species from a seasonally dry tropical forest under drought stress and recovery. *Plant Physiology and Biochemistry, 147*, 181-190. https://doi.org/10.1016/j.plaphy.2019.12.018.

Beckmann, M., Bruelheide, H., & Erfmeier, A. (2011). Germination responses of three grassland species differ between native and invasive origins. *Ecological Research, 26*, 763–771 doi:10.1007/s11284-011-0834-3

Betekhtina, A. A., Ronzhina, D. A., Ivanova, L. A., Malygin, M. V., & Ivanov, L. A. (2019). Relative Growth Rate and Its Components in Invasive Species Heracleum sosnowskyi and Congeneric Native Species H. sibiricum. R*ussian Journal of Biological Invasions, 10*(1), 5–11. https://doi.org/10.1134/S207511171901003X

Betts, A. K. (2011). Vermont climate change indicators. *Weather, Climate, and Society, 3*(2), 106-115. https://doi.org/10.1175/2011WCAS1096.1

Beyen, M. T., & Jain, S. (2015). Wintertime weather-climate variability and its links to early spring ice-out in Maine lakes. *Limnology and Oceanography, 60*(6), 1890-1905. doi: 10.1002/lno.10148

Blossey, B., & Nötzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology, 83*, 887-889

Buckley, Y.M., Briese, D.T. & Rees, M. (2003). Demography and management of the invasive plant species Hypericum perforatum. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology, 40*, 481-493. https://doi.org/10.1046/j.1365-2664.2003.00821.x

Burton, P.J., Jentsch, A., & Walker, L.R. (2020). The Ecology of Disturbance Interactions. *BioScience*, *70*(10), 854-870. https://doi.org/10.1093/biosci/biaa088

Callaway, R.M. and Ridenour, W.M. (2004), Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment, 2*, 436-443. https://doi.org/10.1890/1540-9295(2004)002[0436:NWISAT]2.0.CO;2

Campbell, M.H. (1985). Germination, emergence and seedling growth of Hypericum perforatum L. *Weed Research, 25*, 259-266. https://doi.org/10.1111/j.1365-3180.1985.tb00643.x

Carlyle, C. N., Fraser, L. H., & Turkington, R. (2014). Response of grassland biomass production to simulated climate change and clipping along an elevation gradient. *Oecologia, 174*(3), 1065–1073. https://doi.org/10.1007/s00442-013-2833-2

Cheng, C., Liu, Z., Song, W., Chen, X., Zhang, Z., Li, B., van Kleunen, M., & Wu, J. (2024). Biodiversity increases resistance of grasslands against plant invasions under multiple environmental changes. *Nature communications, 15*(1), 4506. https://doi.org/10.1038/s41467-024-48876-z

Clark, N. (1953). The biology of Hypericum perforatum L. var. angustifolium DC (St. John's Wort) in the Ovens Valley, Victoria, with particular reference to entomological control. *Australian Journal of Botany, 1*(1), 95 10.1071/BT9530095

Clements, D. R. (2017). "*Invasive weed species and their effects.*" in Integrated Weed Management for Sustainable Agriculture, ed R. Zimdahl (Cambridge, UK: Burleigh Dodds Science Publishing), 65–88.

Clements, D. R., & Jones, V. L. (2021). Rapid Evolution of Invasive Weeds Under Climate Change: Present Evidence and Future Research Needs. Frontiers in Agronomy, 3, 664034. https://doi.org/10.3389/fagro.2021.664034

Clements, D.R., & DiTommaso, A. (2011). Climate change and weed adaptation: can evolution of invasive plants lead to greater range expansion than forecasted? Weed Research, 51, 227-240. https://doi.org/10.1111/j.1365-3180.2011.00850.x

Coates, E. (2008). *Hypericum perforatum (Common St. Johnswort) in the Quabbin Reservoir: relationship with the seed bank, growth variables, historical spread and the possibility for impact.* (Adv. M.F. Hoopes).

Colautti, R. I. and H. J. MacIsaac. (2004). A neutral terminology to define 'invasive' species. *Diversity and Distributions*, *10,* 135-141.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. and MacIsaac, H.J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters, 7*, 721-733. https://doi.org/10.1111/j.1461-0248.2004.00616.x

Collins, S.L. (2000). Disturbance Frequency and Community Stability in Native Tallgrass Prairie. *American Naturalist, 155*(3), 311-325. doi: 10.1086/303326.

Crausbay, S. D., Ramirez, A. R., Carter, S. L., Cross, M. S., Hall, K. R., Bathke, D. J., Betancourt, J. L., Colt, S., Cravens, A. E., Dalton, M. S., Dunham, J. B., Hay, L. E., Hayes, M. J., McEvoy, J., McNutt, C. A., Moritz, M. A., Nislow, K. H., Raheem, N., & Sanford, T. (2017). Defining Ecological Drought for the Twenty-First Century. *Bulletin of the American Meteorological Society, 98*(12), 2543-2550. https://doi.org/10.1175/BAMS-D-16-0292.1

Crompton, C.W., Hall, I.V., Jensen, K.I.N., & Hilderbrand, P.D. (1988). The biology of Canadian weeds. 83. Hypericum perforatum L. *Canadian Journal of Plant Science, 68*(1), 149-162.

Davies, K.W., Svejcar, T.J., & Bates, J.D. (2009). Interaction of historical and nonhistorical disturbances maintains native plant communities. *Ecological Applications, 19,* 1536-1545. https://doi.org/10.1890/09-0111.1

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology, 88*(3), 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Davis, M. A., & Thompson, K. (2000). Eight Ways to Be a Colonizer; Two Ways to Be an Invader: A Proposed Nomenclature Scheme for Invasion Ecology. *Bulletin of the Ecological Society of America, 81*(3), 226–230. http://www.jstor.org/stable/20168448

Dekker, J. (2005). *Biology and anthropology of plant invasions.* In Inderjit (Ed.), Invasive Plants: Ecological and Agricultural Aspects (pp. 235–250). Birkhäuser-Verlag. https://doi.org/10.1007/3-7643-7380-6_15

Del Tredici, P. (1977). The Buried Seeds of Comptonia peregrina, the Sweet Fern. *Bulletin of the Torrey Botanical Club*, *104*(3), 270-275. https://doi.org/10.2307/2484309

Descamps, C., Quinet, M., & Jacquemart, A. (2021). The effects of drought on plant–pollinator interactions: What to expect? *Environmental and Experimental Botany,* 182. https://doi.org/10.1016/j.envexpbot.2020.104297.

Dlugosch, K. M., Alice Cang, F., Barker, B. S., Andonian, K., Swope, S. M., & Rieseberg, L. H. (2015). Evolution of invasiveness through increased resource use in a vacant niche. *Nature Plants, 1*(6), 15066. https://doi.org/10.1038/nplants.2015.66

Dunwiddie, P.W., Zaremba, R.E., & Harper, K. A. (1996). A classification of coastal heathlands and sandplain grasslands in Massachusetts. *Rhodora, 98*(894), 117-145.

D'Antonio, C.M., & Vitousek, P.M. (1992). Biological Invasions by Exotic Grasses, the Grass/Fire Cycle, and Global Change. *Annual Review of Ecology, Evolution, and Systematics, 23*, 63-87. https://doi.org/10.1146/annurev.es.23.110192.000431

Elton, C.S. (1958). *The ecology of invasions by plants and animals.* Methuen & Co. Ltd. https://doi.org/10.1007/978-3-030-34721-5

Evans, A. E., Jarnevich, C. S., Beaury, E. M., Engelstad, P. S., Teich, N. B., LaRoe, J. M., & Bradley, B. A. (2024). Shifting hotspots: Climate change projected to drive contractions and expansions of invasive plant abundance habitats. *Diversity and Distributions, 30*(1), 41–54. https://doi.org/10.1111/ddi.13787

Felker-Quinn, E., Schweitzer, J.A., & Bailey, J.K. (2013). Meta‐analysis reveals evolution in invasive plant species but little support for Evolution of Increased Competitive Ability (EICA). *Ecology and Evolution, 3*(3), 739-751. https://doi.org/10.1002/ece3.488

Fensham, R.J., Silcock, J.L. & Dwyer, J.M. (2011). Plant species richness responses to grazing protection and degradation history in a low productivity landscape. *Journal of Vegetation Science, 22*, 997-1008. https://doi.org/10.1111/j.1654-1103.2011.01305.x

Finch, D. M., Butler, J. L., Runyon, J. B., Fettig, C. J., Kilkenny, F. F., Jose, S., Frankel, S. J., Cushman, S. A., Cobb, R. C., Dukes, J. S., Hicke, J. A., & Amelon, S. K. (2021). *Effects of Climate Change on Invasive Species.* In T. M. Poland, T. Patel-Weynand, D. M. Finch, C. F. Miniat, D. C. Hayes, & V. M. Lopez (Eds.), Invasive Species in Forests and Rangelands of the United States (pp. 57–83). Springer International Publishing. https://doi.org/10.1007/978-3-030-45367-1_4

Firn, J., Macdougall, A.S., Schmidt, S., & Buckley, Y.M. (2010). Early emergence and resource availability can competitively favour natives over a functionally similar invader. *Oecologia, 163*(3), 775-84. https://doi.org/10.1007/s00442-010-1583-7

Flickinger, H. D., & Dukes, J. S. (2024). A Review of Theory: Comparing Invasion Ecology and Climate Change‐Induced Range Shifting. *Global Change Biology, 30*(12), e17612. https://doi.org/10.1111/gcb.17612

Foster, D.R. (1992). Land-Use History (1730-1990) and Vegetation Dynamics in Central New England, USA. *Journal of Ecology, 80*(4), 753-771.

Fraterrigo, J.M. and Rusak, J.A. (2008), Disturbance-driven changes in the variability of ecological patterns and processes. *Ecology Letters, 11*, 756-770. https://doi.org/10.1111/j.1461-0248.2008.01191.x

Gelbard, J. L., & Harrison, S. (2005). Invasibility of Roadless Grasslands: An Experimental Study of Yellow Starthistle. *Ecological Applications, 15*(5), 1570–1580. http://www.jstor.org/stable/4543464

Gilbert, B., & Lechowicz, M.J. (2005). Invasibility and Abiotic Gradients: The Positive Correlation between Native and Exotic Plant Diversity. *Ecology, 86*(7), 1848-1855. http://www.jstor.org/stable/3450628

Gilliam, F.S. (2016). Forest ecosystems of temperate climatic regions: from ancient use to climate change. *New Phytologist, 212*, 871-887. https://doi.org/10.1111/nph.14255

Godoy, O., Valladares, F., & Castro-Díez, P. (2011). Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Functional Ecology, 25*(6), 1248-1259. http://www.jstor.org/stable/41319621

Groenteman, R., Fowler, S.V., & Sullivan, J.J. (2011). St. John's wort beetles would not have been introduced to New Zealand now: A retrospective host range test of New Zealand's most successful weed biocontrol agents. *Biological Control, 57*(1), 50-58. https://doi.org/10.1016/j.biocontrol.2011.01.005.

Guiaşu, R.C., & Tindale, C.W. (2023). Logical fallacies persist in invasion biology and blaming the messengers will not improve accountability in this field: a response to Frank et al. *Biology and Philosophy, 38*(3). https://doi.org/10.1007/s10539-023-09892-3

Haeuser E, Dawson W., van Kleunen M. (2018). Introduced garden plants are strong competitors of native and alien residents under simulated climate change. *Journal of Ecology, 107*, 1328-1342. https://doi.org/10.1111/1365-2745.13101

Haeuser, E., Dawson, W. & van Kleunen, M. (2017). The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. *Journal of Ecology, 105*, 1698-1708. https://doi.org/10.1111/1365-2745.12798

Harris, G.A. (1951). *St. Johnswort on western ranges: (A review of literature and bibliography)*. Station Paper No. 26. [Missoula, MT]: U.S. Department of Agriculture, Forest Service, Northern Rocky Mountain Forest and Range Experiment Station. 18 p.

Harris, J.A., & Gill, A.M. (1997). History of the introduction and spread of St. John's wort (Hypericum perforatum L.) in Australia. *Plant Protection Quarterly, 12*(2)

Hector, A., Dobson, K., Minns, A., Bazeley-White, E., & Lawton, J.H. (2001). Community diversity and invasion resistance: An experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research 16*, 819-831. https://doi.org/10.1046/j.1440-1703.2001.00443.x

Hess, S.S., Burns, D.A., Boudinot, F.G., Brown-Lima, C., Corwin, J., Foppert, J.D., Robinson, G.R., Rose, K.C., Schlesinger, M.D., Shuford, R.L., Bradshaw, D., & Stevens, A. (2024). New York State Climate Impacts

Assessment Chapter 05: Ecosystems. *Annals of the New York Academy of Sciences, 1542*(1), 253-340. https://doi.org/10.1111/nyas.15203

Hoebeke, R.E. (1993). Establishment of urophora quadrifasciata (diptera: tephritidae) and chrysolina quadrigemina (coleoptera: chrysomelidae) in portions of eastern United States. *Entomological News, 104*(3), 143-152.

Huffaker, C. B., & Kennett, C. E. (1959). A ten-year study of vegetational changes associated with biological control of Klamath weed. *Journal of Range Management, 12*(2), 69-82.

Iannone, B., Carnevale, S., Main, M., Hill, J., McConnell, J., Johnson, S., Enloe, S., Andreu, M., Bell, E., Cuda, J., & Baker, S. (2020). Invasive Species Terminology: Standardizing for Stakeholder Education. *Journal of Extension, 58*(3). https://doi.org/10.34068/joe.58.03.27

James, J. J., & Drenovsky, R. E. (2007). A Basis for Relative Growth Rate Differences Between Native and Invasive Forb Seedlings. *Rangeland Ecology & Management, 60*(4), 395–400. https://doi.org/10.2111/1551-5028(2007)60[395:ABFRGR]2.0.CO;2

Johanson, J.K., Butler, N.R., & Bickford, C.I. (2016). Classifying Northern New England Landscapes for Improved Conservation. *Rangelands, 38*(6), 357-364. https://doi.org/10.1016/j.rala.2016.10.007.

Karmalkar, A. V., & Bradley, R.S. (2017). Consequences of Global Warming of 1.5 °C and 2 °C for Regional Temperature and Precipitation Changes in the Contiguous United States. *PLoS ONE, 12*(1). https://doi.org/10.1371/journal.pone.0168697

Kiesel, L. (2014). Invasive Plants May Adapt to Climate Change Better than Native Species. *BioScience, 64*(7), 640–640. https://doi.org/10.1093/biosci/biu085

Lanta, V., Liancourt, P., Altman, J., Černý, T., Dvorský, M., Fibich, P., Götzenberger, L., Hornych, O., Miklín, J., Petřík, P., Pyšek, P., Čížek, L., & Doležal, J. (2022). Determinants of invasion by single versus multiple plant species in temperate lowland forests. *Biological Invasions, 24*, 2513-2528. https://doi.org/10.1007/s10530-022-02793-8

Lear, L., Padfield, D., Inamine, H., Shea, K., & Buckling, A. (2022). Disturbance‐mediated invasions are dependent on community resource abundance. *Ecology, 103*(8). https://doi.org/10.1002/ecy.3728

Liu, Y., Oduor, A.M.O., Zhang, Z., Manea, A., Tooth, I.M., Leishman, M.R., Xu, X. & van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology, 23*, 3363-3370. https://doi.org/10.1111/gcb.13579

Lustenhouwer, N., Wilschut, R. A., Williams, J. L., Van Der Putten, W. H., & Levine, J. M. (2018). Rapid evolution of phenology during range expansion with recent climate change. *Global Change Biology, 24*(2). https://doi.org/10.1111/gcb.13947

Maron, J.L., & Marler, M. (2007). Native plant diversity resists invasion at both low and high resource levels. *Ecology, 88*, 2651-2661. https://doi.org/10.1890/06-1993.1

Maron, J.L., Elmendorf, S.C., & Vilà, M. (2007). Contrasting Plant Physiological Adaptation to Climate in the Native and Introduced Range of Hypericum perforatum. *Evolution, 61*(8), 1912–1924. http://www.jstor.org/stable/4627007

Maron, J.L., Vilà, M., Bommarco, R., Elmendorf, S., & Beardsley, P. (2004). Rapid Evolution of an Invasive Plant. *Ecological Monographs, 74*(2), 261–280.

Maron, J.L. & Marler, M. (2008). Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology, 96*, 1187-1197. https://doi.org/10.1111/j.1365-2745.2008.01440.x

Marvel, K., W. Su, R. Delgado, S. Aarons, A. Chatterjee, M.E. Garcia, Z. Hausfather, K. Hayhoe, D.A. Hence, E.B. Jewett, A. Robel, D. Singh, A. Tripati, and R.S. Vose, 2023: *Ch. 2. Climate trends*. In: Fifth National Climate Assessment. Crimmins, A.R., C.W. Avery, D.R. Easterling, K.E. Kunkel, B.C. Stewart, and T.K. Maycock, Eds. U.S. Global Change Research Program, Washington, DC, USA. https://doi.org/10.7930/NCA5.2023.CH2

Merow, C., Bois, S. T., Allen, J. M., Xie, Y., & Silander, J. A. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proceedings of the National Academy of Sciences, 114*(16). https://doi.org/10.1073/pnas.1609633114

Miller, M.D. (2025). Local scale climate change variability in New England, United States. *Climatic Change 178*, 12. https://doi.org/10.1007/s10584-024-03850-y

Mingxue, X., Junxi, W., Jiaojiao, W., Yingjie, G., Duo, L., Ying, P., & Xianzhou, Z. (2021). Heavy Grazing Altered the Biodiversity–Productivity Relationship of Alpine Grasslands in Lhasa River Valley, Tibet. *Frontiers in Ecology and Evolution, 9*. doi: 10.3389/fevo.2021.698707

Molins, M. P., Corral, J. M., Aliyu, O. M., Koch, M. A., Betzin, A., Maron, J. L., & Sharbel, T. F. (2014). Biogeographic variation in genetic variability, apomixis expression and ploidy of St. John’s wort (Hypericum perforatum) across its native and introduced range. *Annals of Botany, 113*(3), 417–427. https://doi.org/10.1093/aob/mct268

Morrison, K. D., Reekie, E. G., & Jensen, K. I. N. (1998). Biocontrol of Common St. Johnswort (Hypericum perforatum) with Chrysolina hyperici and a host-specific Colletotrichum gloeosporioides. *Weed Technology, 12*(3), 426-435. doi:10.1017/S0890037X00044092

National Oceanic and Atmospheric Administration. (2019). What is an invasive species? Noaa.gov; National Ocean Service. https://oceanservice.noaa.gov/facts/invasive.html

Nunes, A., Werner, S.S., Boff, M.I.C., Boff, P. (2019). Feasibility in seed germination of Hypericum perforatum L. submitted at different temperatures and treatments with high dilutions. *International Journal of High Dilution Research, 18*(3-4), 2-12. https://doi.org/10.51910/ijhdr.v18i3-4.963

Oakley, C.A. & Knox, J.S. (2013). Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration. *Applied Vegetation Science, 16*, 21-28. https://doi.org/10.1111/j.1654-109X.2012.01202.x

Parendes, L.A., & Jones, J.A. (2000). Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. *Conservation Biology, 14*(1), 64-75.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and systematics, 37,* 637-669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Pearson, D.E., Ortega, Y.K. and Maron, J.L. (2017), The tortoise and the hare: reducing resource availability shifts competitive balance between plant species. *Journal of Ecology, 105,* 999-1009. https://doi.org/10.1111/1365-2745.12736

Prior, K. M., Powell, T.H.Q., Joseph. A.L., & Hellmann, J.J. (2015). Insights from community ecology into the role of enemy release in causing invasion success: the importance of native enemy effects. *Biological Invasions, 17*, 1283-1297. https://doi.org/10.1007/s10530-014-0800-4

Pérez-García, F., Huertas, M., Mora, E., Peña, B., Varela, F., & González-Benito, M.E. (2006). Hypericum perforatum L. seed germination: interpopulation variation and effect of light, temperature, presowing treatments and seed desiccation. *Genetic Resources and Crop Evolution 53*, 1187-1198. https://doi.org/10.1007/s10722-005-2012-3

Randall, C.B., J.E. Andreas, J. Milan, and C.E. Moffat. 2024. *Common St. Johnswort (Hypericum perforatum): History and Ecology in North America.* In: R.L. Winston, Ed. Biological Control of Weeds in North America. North American Invasive Species Management Association, Milwaukee, WI.

Reeves, K. (2010). *Exotic Species: St. Johnswort.* US National Park Service. https://www.nps.gov/articles/st-johnswort.htm#:~:text=Habitat%20and%20Ecology,states%20by%20the%20early%201900s

Robinson, A., Lehmann, J., Barriopedro, D., Rahmstorf, S & Coumou, D. (2021). Increasing heat and rainfall extremes now far outside the historical climate. *NPJ Climate and Atmospheric Science 4*(45). https://doi.org/10.1038/s41612-021-00202-w

Rustad, L., Campbell, J., Dukes, J. S., Huntington, T., Lambert, K. F., Mohan, J., & Rodenhouse, N. (2011). *Changing Climate, Changing Forests: The Impacts of Climate Change on Forests of the Northeastern United States and Eastern Canada.* USDA.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., & Wall, D.H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science, 287*(5459), 1770-1774. doi: 10.1126/science.287.5459.1770

Salonen, A.O., Reiser, D. (2023). *Climate Change.* In: Idowu, S.O., Schmidpeter, R., Capaldi, N., Zu, L., Del Baldo, M., Abreu, R. (eds) Encyclopedia of Sustainable Management. https://doi.org/10.1007/978-3-031-25984-5_75

Sampson, A.W., & Parker, K.W. (1930). *St. Johnswort on range lands of California.* Bulletin 503. Berkeley, CA: University of California, College of Agriculture, Agriculture Experiment Station. 47 p.

Schuster, M.J., Wragg, P.D., Williams, L.J., Butler, E.E., Stefanski, A., & Reich, P.B. (2020). Phenology matters: Extended spring and autumn canopy cover increases biotic resistance of forests to invasion by common buckthorn (Rhamnus cathartica). *Forest Ecology and Management, 464*. https://doi.org/10.1016/j.foreco.2020.118067

Sheahan, C.M. (2012). *Fact sheet for common St. Johnswort (Hypericum perforatum)*. USDA-NRCS, Cape May Plant Materials Center, Cape May, NJ.

Shivanna, K. R. (2022). Climate change and its impact on biodiversity and human welfare. *Proceedings of the Indian National Science Academy, 88*(2), 160–171. https://doi.org/10.1007/s43538-022-00073-6

Spinoni, J., Vogt, J.V., Naumann, G., Barbosa, P. and Dosio, A. (2018). Will drought events become more frequent and severe in Europe? *International Journal of Climatology, 38*, 1718-1736. https://doi.org/10.1002/joc.5291

Staines, C. L., & S. L. Staines. (2006). Additional Eastern U.S. Records of the Introduced Leaf Beetle Chrysolina quadrigemina (Suffrian) (Coleoptera: Chrysomelidae). *The Coleopterists Bulletin, 60*(1), 72–72. http://www.jstor.org/stable/4009970

Sultan, S.E. (2003). Phenotypic plasticity in plants: a case study in ecological development. *Evolution & Development, 5*, 25-33. https://doi.org/10.1046/j.1525-142X.2003.03005.x

Sun, Y., Ren, Z., Müller-Schärer, H., Callaway, R.M., van Kleunen, M., & Huang, W. (2024). Increasing and Fluctuating Resource Availability Enhances Invasional Meltdown. *Ecology, 105*(9). https://doi.org/10.1002/ecy.4387

Tanentzap, A. J., & Kolmakova, O. (2023). Global change ecology: Science to heal a damaged planet. *PLoS biology, 21*(12). https://doi.org/10.1371/journal.pbio.3002455

Tingle, J. L., Cook-Patton, S. C., & Agrawal, A. A. (2016). Spillover of a biological control agent (Chrysolina quadrigemina) onto native St. Johnswort (Hypericum punctatum). *PeerJ, 4.* https://doi.org/10.7717/peerj.1886

Tisdale, E.W., Hironaka, M., & Pringle, W.L. (1959). Observations on the autecology of Hypericum perforatum. *Ecology, 40*(1), 54-62.

Turner, M.G. (2010), Disturbance and landscape dynamics in a changing world. *Ecology, 91*, 2833-2849. https://doi.org/10.1890/10-0097.1

USDA. (2018). *St. Johnswort (Hypericum perforatum).* https://www.ars.usda.gov/pacific-west-area/logan-ut/poisonous-plant-research/docs/st-johnswort-hypericum-perforatum/

USDA. (2025). *Hypericum punctatum plant profile.* https://plants.sc.egov.usda.gov/plant-profile/HYPU/characteristics

Valéry, L., Fritz, H., Lefeuvre, J., & Simberloff, D. (2008). In search of a real definition of the biological invasion phenomenon itself. *Biological Invasions, 10*, 1345-1351. https://doi.org/10.1007/s10530-007-9209-7

Van Driesche, R.G., Carruthers, R.I., Center, T., Hoddle, M.S., Hough-Goldstein, J., Morin, L., Smith, L., Wagner, D.L., Blossey, B., Brancatini. V., Casagrande, R., Causton, C.E., Coetzee, J.A., Cuda, J., Ding, J., Fowler, S.V., Frank, J.H., Fuester, R., Goolsby, J., Grodowitz, M., Heard, T.A., Hill, M.P., Hoffmann, J.H., Huber, J., Julien, M., Kairo, M.T.K., Kenis, M., Mason, P., Medal, J., Messing, R., Miller, R., Moore, A., Neuenschwander, P., Newman, R., Norambuena, H., Palmer, W.A., Pemberton, R., Perez Panduro, A., Pratt, P.D., Rayamajhi, M., Salom, S., Sands, D., Schooler, S., Schwarzländer, M., Sheppard, A., Shaw, R., Tipping, P.W., van Klinken, R.D. (2010). Classical biological control for the protection of natural ecosystems. *Biological Control, 54*, S2-S33.https://doi.org/10.1016/j.biocontrol.2010.03.003.

Van Kleunen, M. and Schmid, B. (2003). No evidence for an evolutionary increased competitive ability in an invasive plant. *Ecology, 84*, 2816-2823. https://doi.org/10.1890/02-0494

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters, 14*, 702-708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Vila, M., Gomez, A., & Maron, J.L. (2003). Are alien plants more competitive than their native conspecifics? A test using Hypericum perforatum L. *Oecologia, 137*, 211-215.

Vilà, M., Maron, J.L. & Marco, L. (2005). Evidence for the enemy release hypothesis in Hypericum perforatum. *Oecologia, 142*, 474-479. https://doi.org/10.1007/s00442-004-1731-z

Walker, L., Sirvent, T., Gibson, D., & Vance, N. (2001). Regional differences in hypericin and pseudohypericin concentrations and five morphological traits among Hypericum perforatum plants in the northwestern United States. *Canadian Journal of Botany, 79*(10), 1248-1255.

Walsh, J.E., Ballinger, T.J., Euskirchen, E.S., Hanna, E., Mård, J., Overland, J.E., Tangen, H., & Vihma, T. (2020). Extreme weather and climate events in northern areas: A review. *Earth-Science Reviews, 209*. https://doi.org/10.1016/j.earscirev.2020.103324.

Warr, S.J., Kent, M., & Thompson, K. (1994). Seed bank composition and variability in five woodlands in south-west England. *Journal of Biogeography, 21*(2), 151-168.

White, P.S., & Pickett, S.T.A. (1985). Chapter 1 - Natural Disturbance and Patch Dynamics: An Introduction. *The Ecology of Natural Disturbance and Patch Dynamics*, Academic Press, 1985, 3-13. ISBN 9780125545204. https://doi.org/10.1016/B978-0-12-554520-4.50006-X.

Williams, J. L., Hufbauer, R. A., & Miller, T. E. X. (2019). How Evolution Modifies the Variability of Range Expansion. *Trends in Ecology & Evolution, 34*(10), 903–913. https://doi.org/10.1016/j.tree.2019.05.012

Williams, J. L., Kendall, B. E., & Levine, J. M. (2016). Rapid evolution accelerates plant population spread in fragmented experimental landscapes. *Science, 353*(6298), 482–485. https://doi.org/10.1126/science.aaf6268

Williams, K.S. (1984). Climactic influences on weeds and their herbivores. *Agriculture of Canada, 127-132.*

Willis, C. G., Ruhfel, B. R., Primack, R. B., Miller-Rushing, A. J., Losos, J. B., & Davis, C. C. (2010). Favorable Climate Change Response Explains Non-Native Species' Success in Thoreau's Woods. *PLoS one, 5*(1). https://doi.org/10.1371/journal.pone.0008878

Wu, Y., Du, Y., Liu, X., Wan, X., Yin, B., Hao, Y., & Wang, Y. (2023). Grassland biodiversity response to livestock grazing, productivity, and climate varies across biome components and diversity measurements. *Science of The Total Environment, 878*. https://doi.org/10.1016/j.scitotenv.2023.162994.

Xavier, R. D. O., Leite, M. B., & Da Silva Matos, D. M. (2019). Phenological and reproductive traits and their response to environmental variation differ among native and invasive grasses in a Neotropical savanna. *Biological Invasions, 21*(8), 2761–2779. https://doi.org/10.1007/s10530-019-02013-w

Xiang, M., Wu, J., Wu, J., Guo, Y., Lha, D., Pan, Y., & Zhang, X. (2021). Heavy Grazing Altered the Biodiversity–Productivity Relationship of Alpine Grasslands in Lhasa River Valley, Tibet. *Frontiers in Ecology and Evolution, 9*. https://doi.org/10.3389/fevo.2021.698707

Yanelli, F.A., MacLaren, C., Kollmann, J. (2020). Moving away from limiting similarity during restoration: timing of arrival and native biomass are better proxies of invasion suppression in grassland communities. *Frontiers in Ecology and Evolution, 8.* https://doi.org/10.3389/fevo.2020.00238

Yannelli, F.A., Coch, C., Jeschke, J.M., & Kollmann, J. (2017). Limiting similarity and Darwin's naturalization hypothesis: understanding the drivers of biotic resistance against invasive plant species. *Oecologia 183*, 775-784. https://doi.org/10.1007/s00442-016-3798-8

Young, S. S., & Young, J. S. (2021). Overall Warming with Reduced Seasonality: Temperature Change in New England, USA, 1900–2020. *Climate, 9*(12).

Yu, H., Han, C., Ren, G., Wu, X., Qi, S., Yang, B., Cui, M., Fan, X., Zhu, Z., Dai, Z., & Du, D. (2024). Heat Wave Adaptations: Unraveling the Competitive

Dynamics Between Invasive Wedelia trilobata and Native Wedelia chinensis. *Plants, 13*(24), 3480. https://doi.org/10.3390/plants13243480

Zhang, Z., Zhou, F., Pan, X., van Kleunen, M., Liu, M., & Li, B. (2019). Evolution of increased intraspecific competitive ability following introduction: The importance of relatedness among genotypes. *Journal of Ecology, 107*, 387-395. https://doi.org/10.1111/1365-2745.13016

Zouhar, Kris. (2004). *Hypericum perforatum*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer).