Ecological Impacts and Phenotypic Plasticity of a Global Invasive Cactus, *Opuntia ficus-indica*

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List of publications included in this dissertation

This thesis is based on the following three studies, which are referred to in the text as chapters with their respective Roman numerals:

Chapter I

Yohannes B. Tesfay and Juergen Kreyling (2021)

"The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea", *Biological Invasions* 23, 433–442 (2021). https://doi.org/10.1007/s10530-020-02373-8

Chapter II

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Chapter III

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Author contributions

Thesis summary: Written by Yohannes B. Tesfay

Yohannes B. Tesfay developed an original research proposal and improved the research project with the advice of Jürgen Kreyling.

Chapter I

Yohannes B. Tesfay conceived and designed the study with the guidance and advice of Jürgen Kreyling, Yohannes B. Tesfay performed the field work and collected field data. Jürgen Kreyling and Yohannes B. Tesfay analysed the data. Yohannes B. Tesfay and Jürgen Kreyling contributed to the interpretation of the results. Yohannes B. Tesfay led the writing of the manuscript.

Chapter II

Yohannes B. Tesfay and Jürgen Kreyling conceived and designed the study. Yohannes B. Tesfay performed the lab/ experimental work. Pretrials of the experiment were performed by Annika Blaschke, as a Bachelor thesis under the supervision of Yohannes B. Tesfay. Yohannes B. Tesfay did the statistical analyses with advice from Jürgen Kreyling; Annika Blaschke performed the analysis of the pretrials with the advice of Yohannes B. Tesfay. Yohannes B. Tesfay and Jürgen Kreyling contributed to the interpretation of the results. All authors commented on the manuscript. Yohannes B. Tesfay led the writing of the manuscript.

Chapter III

Yohannes B. Tesfay and Jürgen Kreyling conceived and designed the study. Yohannes B. Tesfay performed the experiment with contributions by Nathan Ashley (DAAD RISE Internship) and Annika Blaschke (Bachelor thesis). Yohannes B. Tesfay did the statistical analyses with advice from Jürgen Kreyling. Benziane Adli, Liberato Martinez and Alessio Scalisi provided the seeds and necessary information regarding their sources. Pretrials of the experiment were performed by Annika Blaschke. Yohannes B. Tesfay and Jürgen Kreyling contributed to the interpretation of the results. All authors commented on the manuscript. Yohannes B. Tesfay led the writing of the manuscript.

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Abstract

Biological invasions by non-native species pose one of the major threats to biodiversity, the way ecosystems function, and the well-being of humans. These invasions can occur through various means, including accidental or intentional introductions by humans, natural dispersal, and climate change. Non-native species can harm the native species and ecosystems, by homogenizing plant communities, competing for resources, changing how the ecosystem operates, and eventually causing native species to go extinct. Even though not all non-native species become invasive, changes in climate and ecosystems can cause the successful establishment and spread of non-native species. Despite the advancements in our understanding of biological invasions in recent years, research has been biased towards temperate regions, whereas arid and semi-arid regions that are highly impacted by climate change are underrepresented. Thus, particularly focusing on the impacts of biological invasions in subtropical arid and semi-arid regions, the goal of this PhD project was to explore the effects of an invasive cactus on the local native communities and investigate the mechanisms of its successful invasion. Certain species are found to take advantage of the ever-drying climates in the arid/ semi-arid regions of the world. *Opuntia ficus-indica*, native to Mexico, is an exceptionally successful drought-tolerant invasive cactus that successfully grows in these regions. *O. ficus-indica*, a most widespread invasive cactus, is considered an ecosystem engineer as it modifies the habitats of indigenous plant species and dependent animals. This project aimed to identify the ecological impacts of *O. ficus-indica* in the highlands of Eritrea, the competitive potential of *O. ficus-indica* and the plastic changes that enabled its spread and invasion (**Chapters I-III**). For this purpose, field observations and common garden experiments were carried out throughout the project.

We investigated the effects of *Opuntia ficus-indica* on the spatial diversity of native plant communities (**Chapter I**), its competitive ability against native species (**Chapter II**) and the phenotypic plasticity of *O. ficus-indica* (**Chapter III**). To investigate the main ecological effects of *O. ficus-indica* on the native community, field data was collected from the highlands of Eritrea and comparisons were made between *O. ficus-indica* invaded and non-invaded areas (**Chapter I**). The study aimed to understand the effects of *O. ficus-indica* by examining species composition, richness, and diversity across vegetation layers and revealed that *O. ficus-indica* homogenises the species composition of the native ecosystem. This provides evidence that the presence of *O. ficus-indica* reduces landscape-level heterogeneity

or spatial diversity. However, *O. ficus-indica* did not influence the species richness and diversity of the local communities. The mechanisms of the successful homogenisation of the local communities by *O. ficus-indica* were attributed to the potential competitive abilities of *O. ficus-indica* against the native species, and the plastic and adaptive traits it developed in the non-native ranges. The first assumption was tested by setting up a common garden competition experiment between two native Eritrean species, *Ricinus communis* and *Solanum marginatum* (**Chapter II).** The experiment used two water availability treatments, wet and dry, and categorized plants into intraspecific (native or invasive only) and interspecific (native and invasive) competition. The study evaluated the impacts by comparing the growth of *O. ficus-indica* alone to the growth alongside native species which revealed the weak competitive potential of *O. ficus-indica*. However, *O. ficus-indica* was observed to outgrow the native species in several folds which can be attributed to its successful invasion. The second assumption of the successful spread of *O. ficus-indica* was attributed to the phenotypic plastic traits adapted by *O. ficus-indica* in the non-native ranges (**Chapter III**). The phenotypic plasticity of *O. ficus-indica* was assessed by exposing it to water stress across dry and wet environments. The species were cultivated from a diverse set of 12 populations, encompassing its native range in Mexico with three cultivars and non-native ranges in Africa (Algeria, Eritrea, Ethiopia), the island of Madeira off the coast of Africa, and in Europe, Italy with two cultivars and in Portugal from three sites. In Mexico and Italy, we collected various cultivars to ensure a wide representation of genotypes. We found that the species originating from the native range of *O. ficus-indica* exhibited lower plasticity to conditions of elevated water availability. Furthermore, a trial gradient experiment on *O. ficus-indica* was conducted to determine the appropriate watering levels for the species and the experiment revealed not only the species' capacity to endure a lack of water for nine months but also its ability to withstand prolonged waterlogged conditions.

This thesis illustrates the fact that invasive species are a major threat to biodiversity and ecosystem functioning worldwide, especially in rarely studied regions with dry climates and limited resources. How can invasive plants spread and cause negative impacts on native ecosystems (Chapter I), despite their weak competitive abilities (Chapter II)? This thesis explored these questions by examining the case of *O. ficus-indica*, an invasive species in arid/ semi-arid climates (Chapter I). It showed that *O. ficus-indica* has a high growth potential that allows it to overcome resource limitations, that its growth is not affected by competition from native species (Chapter II), and that it exhibits adaptive plasticity that

enhances its invasion success in different environments (Chapter III). This thesis revealed the complex mechanisms and consequences of biological invasions in dry climates and contributes to the understanding of invasive species. It also suggests that more research is needed in understudied regions to assess the impacts of *O. ficus-indica* or invasive species in general on native biodiversity and ecosystem services and to identify the factors that influence the competitive and adaptive potentials.

Thesis Summary

Introduction

Biological invasions are considered one of the major drivers of global change and biodiversity loss, as well as a threat to human health and animal well-being (Elsheikh et al. 2021; Ozaslan et al. 2016). These invasions can occur through a variety of mechanisms, including unintentional or intentional human introductions, natural dispersal, and climate change (McKinney and Lockwood 1999; Pyšek et al. 2022; Staples 2001). Invasive plants in particular have attracted significant attention due to their substantial economic implications as problematic weeds and their potential to detrimentally impact native biodiversity and ecosystems by homogenizing plant communities, competing for resources, altering ecosystem functions, and eventually driving native species extinct (Daehler 1998; Vilà et al. 2011; Wilcove et al. 1998). Even if not all non-native species become invasive, changes in climate and ecosystems can result in the successful establishment and proliferation of non-native species (Holenstein et al. 2021; Williamson 1996).

The success of invasive species depends upon several ecological factors, prominently including their competitive potential, environmental tolerance, and phenotypic plasticity (Gioria and Osborne 2014; Zerebecki and Sorte 2011). Competitive abilities, for instance, play an important role in determining invasion success. According to the Evolution of Increased Competitive Ability hypothesis (Hierro et al. 2022), invasive plants tend to exhibit enhanced competitive abilities compared to their native counterparts. This advantage often stems from their strategic resource allocation, prioritizing growth over defence. It is noteworthy, however, that the extent of their competitive advantage can vary depending on the identity of competing species and the prevailing environmental conditions counterparts (Zheng et al. 2015). In the context of environmental change, invasive species often display a notable advantage. As global temperatures rise due to climate change, invasive species are predicted to outperform native species. This advantage is largely attributed to the broader and more robust physiological tolerances observed in many invasive species. These expanded tolerances allow invasive species to thrive and adapt more effectively to changing environmental conditions. (Zerebecki and Sorte 2011).

Furthermore, the phenomenon of phenotypic plasticity significantly influences invasive species' success. Invasive plants frequently exhibit plastic responses to novel selection pressures encountered in new environments, thereby enhancing their local fitness and competitive edge against native species (Funk 2008). Numerous studies have supported a

positive correlation between phenotypic plasticity and invasive ability. However, it is crucial to acknowledge that while high phenotypic plasticity contributes to adaptability, its direct relationship with overall fitness and its relative importance compared to other factors remain subjects of ongoing research (Matzek 2012; Zhang et al. 2022).

Despite recent advances in our understanding of biological invasions, research has been biased towards temperate regions, leaving sub-tropical arid and semi-arid regions, which are heavily impacted by climate change, underrepresented (Akomolafe and Rosazlina 2023). Only limited studies have been done on invasive species in Africa. The Invasive Woody Plant Database with over 5000 publications on species invasiveness has only 6% referring to tropical Africa (Obiri 2011). This indicates that the pressure of exotic species on the native diversity in these regions has rarely been studied.

Arid and semi-arid regions (drylands) cover about 40% of the land surface in the world and the coverage is increasing due to climate change. These regions are characterized by low and fluctuating resources, high evaporation rates, and extreme temperatures (Burrell et al. 2020; Gong et al. 2016; Pearson et al. 2018). They are also home to a rich diversity of plant and animal species that have adapted to harsh environmental conditions (Maestre et al. 2012). However, these regions are also vulnerable to degradation by invasive species, wildfire, overgrazing and agricultural conversion. These disturbances and others are accelerated by decreasing water availability due to drought and elevated temperatures that are projected to become more pronounced (Fensholt et al. 2012; Huang et al. 2020). Such ecosystems with fluctuating resources that provide temporary access of resources are vulnerable to invasion than ecosystems that never provide free resources due to their stable conditions, and this leads to strong competition (Pearson et al. 2018).

One of the countries situated in this dryland section of the world is Eritrea. Eritrea's climate exhibits a diverse range, spanning from hot and arid conditions adjacent to the Red Sea to temperate climates within isolated micro-catchments. Annual precipitation increases from the northern to southern regions, varying from less than 200 mm in the northwest lowlands to over 700 mm in the southwest lowlands. Precipitation generally rises with altitude, resulting in approximately 50% of the country receiving less than 300 mm, 40% receiving between 300 and 600 mm, and 10% receiving more than 600 mm of rainfall annually (Fao 1994; Haile et al. 1988). In terms of temperature, around 70% of Eritrea is categorized as hot to very hot with mean annual temperatures exceeding 27°C, about 25% experiences warm to mild conditions with a mean temperature of approximately 22°C, and the remaining

5% falls into the cool category with mean annual temperatures below 19°C (Ogbazghi and Stillhardt 2011). Habtemichael's (2004) climate classification encompasses distinct regions, including coastal, eastern lowland, eastern escarpment, highland, western escarpment, and western lowland climates. Moreover, the vegetation map of Africa according to White (1983), initially produced to record the areas across the continent that gave rise to clusters of distinct species, referred to as regional centres of endemism, had 20 major regional centres of endemism (Fig. 1). Among these regional centres of endemism, Eritrea represents four, namely, Sudanian, Somali-Masai, Afromontane, and Sahel regions (Friis 1992; White 1983).
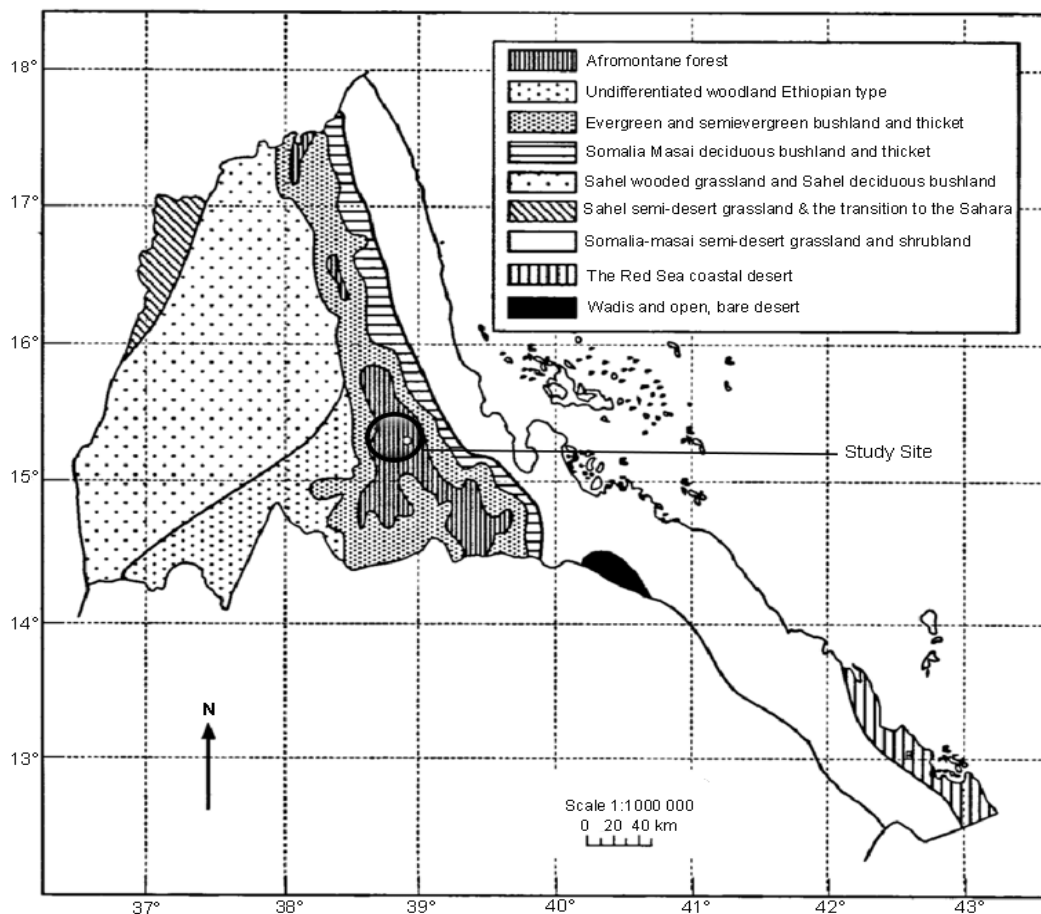

Fig. 1. The vegetation map of Eritrea (Ogbazghi 2001) adapted from White's (1983) vegetation map of Africa. This map also indicates the study site where the field data for this project were collected.

A highly invasive cactus species, *Opuntia ficus-indica*, covers an estimated 10,000 hectares in this highland, particularly on the eastern escarpments. Although the exact time of its

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introduction to Eritrea is unclear, it is believed to have been planted in the southern highlands as early as 1839 before spreading to the central highlands (Bein et al. 1996). These highlands which are part of the Afromontane vegetation type, are considered one of the major regional centres of endemism (White 1983), and it is here the invasive *O. ficus-indica* poses a threat to the ecological functioning of these native communities. As stated above, there is a lack of comparable studies that investigate the impacts of such invasive species on the local communities (**Chapter I**).

Study species

Opuntia ficus-indica, a cactus species belonging to the Cactaceae family, is of significant economic importance worldwide. It is believed to have originated in central Mexico and was brought to the Iberian Peninsula by Spanish conquerors between the 15th and 16th centuries (Barbera et al. 1992; Reis et al. 2018), eventually spreading throughout the Mediterranean Basin (Le Houérou 1996; Reis et al. 2018). Today, it is found in various countries across the Americas, Australia, Europe, Africa, and Asia (Novoa et al. 2014). Known for its adaptability to highly stressful growing conditions, *O. ficus-indica* has multiple uses in agroindustry, including its large, sweet fruits, which are sources of functional compounds. The plant is also used for cattle and sheep feeding, as a green vegetable called "nopalitos" in Mexico, for cochineal dye production, and as a medicinal plant (Salem and Smith 2008). Additionally, it has potential applications in erosion control, land rehabilitation, and as a carbon sink (Nobel and Bobich 2002).

Opuntia ficus-indica has several traits that make it a successful invader, such as rapid growth rate, high reproductive output, vegetative propagation, tolerance to drought and salinity, and resistance to herbivory (Gajender et al. 2014; Oduor et al. 2018). It can also form dense monocultures that exclude other plants and create fire hazards (Brooks et al. 2004). Moreover, it can benefit from mutualistic interactions with other invasive species, such as ants that disperse its seeds (Acuña-Soto et al. 2023) and cochineal insects that produce a valuable dye from its sap (Tovar et al. 2005). *O. ficus-indica* can have negative impacts on native plant diversity at different spatial scales. It is considered an ecosystem engineer (Jones et al. 1994) as it modifies the habitats of the indigenous plant species and dependent animals. The presence of *O. ficus-indica* can reduce the abundance and richness of native plants by competing for light, water, and nutrients. Moreover, it can reduce the beta diversity, i.e., the variation in species composition among sites, by homogenizing the flora across different habitats (**Chapter I**). The cladodes with their thorny structures impede the movement of

livestock and humans as they form impenetrable thickets that displace native plants and reduce the carrying capacity of pasture (Obiri 2011).

Impacts and mechanisms of invasive plants

One of the major threats to the sustainability of dryland ecosystems is the invasion of exotic plant species that can alter the natural balance and functioning of native communities. Invasive exotic plants can exploit the temporal and spatial heterogeneity of native species and water availability in arid regions, gaining a competitive advantage over native plants that are adapted to low and stable water regimes (**Chapter I**; Dar and Reshi 2015; Lososová et al. 2016). The invasion of exotic plants can also affect soil properties, fire regimes, and biotic interactions in dryland ecosystems, resulting in negative impacts that hinder the restoration of native vegetation and soil stability (Brooks et al. 2004; Gill et al. 2018; Kumar Rai and Singh 2020). Moreover, invasive exotic plants can displace native perennial vegetation, and suppress species diversity.

These invasive plants have different mechanisms for the mitigation of biotic and abiotic stresses in many introduced or invaded areas. It seems that, in their strategy to tolerate biotic and abiotic stresses, invasive plants interact with the native community in such a way that increases their resource acquisition, providing them more opportunities for success, establishment, and dominance (Munns and Millar 2023; Nawaz et al. 2023). Therefore, the recovery of dryland ecosystems after large-scale disturbances, such as fire, drought, or land use change, is a challenging task that requires a comprehensive understanding of the ecological mechanisms and processes that cause the invasion success and impact of exotic plants (Garbowski et al. 2021; Geary et al. 2023).

Invasive plant species possess competitive abilities that contribute to their successful establishment and dominance in new environments. These species often exhibit traits such as rapid growth rates, high reproductive capacity, efficient resource utilization, and a lack of specialized ecological requirements, enabling them to outcompete native or less aggressive plants (Funk and Vitousek 2007). In the novel habitats, invasive species experience increased invasion success as there is the lack of natural enemies as the enemy release hypothesis suggests (Prior et al. 2015). This is therefore considered as a crucial mechanism that can explain why many invasive species are highly competitive outside their native range. In their native range, they are usually held in check by the natural enemies such as herbivores, pathogens, and parasites. Additionally, invasive plants may have traits that

enhance their ability to modify and disrupt ecosystems, altering soil composition and nutrient cycling to their advantage (Ehrenfeld 2003). Conversely, native, or weakly competitive plant species typically lack some of these traits, making them vulnerable to displacement by invasive species. Weak competitors often possess slower growth rates, limited reproductive abilities, and are adapted to specific ecological niches, rendering them less capable of thriving in disturbed or highly competitive environments (Levine et al. 2004). However, it's important to note that not all invasive species are equally competitive, and some may lack the robust competitive traits commonly associated with invasiveness (**Chapter II**; Čuda et al. 2015; Liu et al. 2018).

One of the important strategies for the successful spread of invasive species is the plastic changes they exhibit (**Chapter III**; Richards et al. 2006; Sexton et al. 2002). When an introduced plant species invades a new environment, it faces two fundamental possibilities: either the plant needs to exhibit significant physiological tolerance and plasticity (**Chapter III**), or it must undergo genetic differentiation to attain the necessary levels of fitness for survival and proliferation across diverse environmental conditions (Richardson and Pyšek 2006). Several research studies have proven the significance of phenotypic plasticity versus rapid evolution across a diverse range of systems and taxa (Reznick and Ghalambor, 2001; Bossdorf et al., 2005). Phenotypic plasticity undoubtedly plays a crucial role in the success of numerous invasive species across various taxonomic groups and habitats as seen in species like *Alliaria petiolata* (Hillstrom and Cipollini 2011), Carpobrotus spp. (Weber and D'Antonio 2000), and *Opuntia ficus-indica* (**Chapter III**). Enhanced phenotypic plasticity in invasive *O. ficus-indica* likely supports its success across regions, particularly in less arid conditions. Climate change-driven arid area expansion enhances its adaptability, facilitating survival during droughts and rapid growth in high-water periods, elevating its invasive potential. Species that are found in the introduced ranges are found to show more plastic adaptations than those that are found in the native ranges, e.g., *Senecio inaequidens* (Prati and Bossdorf 2004), *Imperata cylindrica* (Hiatt and Flory 2020) and *O. ficus-indica* (**Chapter III**).

Aims of the thesis and experimental design

This thesis aims to address the knowledge gap of invasive species in a region barely studied by investigating how the environment shapes and responds to the invasion of *Opuntia ficus-indica*, and in turn advance our knowledge of invasive species. By combining ecological field data **(Chapter I)**, competition experiments **(Chapter II)**, and trials on native and

introduced populations (**Chapter III**), this project explored how *O. ficus-indica* adapts to different environmental conditions and how it affects native plant diversity and productivity. The initial phase of ecological field data collection was undertaken in the highlands of Eritrea from June to August 2018, as detailed in Chapter I. Subsequently, the remaining parts of the project were carried out within the controlled environment of a common-garden experiment situated in Greifswald, Germany. The project was structured to first investigate the field-level invasion success of *O. ficus-indica* (**Chapter I**) and then explore into the potential traits that assisted its success through the implementation of common-garden experiments (**Chapters II** and **III**). The cacti for the experiments were cultivated in a climate-controlled greenhouse, maintaining an average 40% humidity and a temperature range of 12°C (for 12 hours at night) to 20°C (for 12 hours a day), with controlled air flow through windows for natural cooling if temperatures exceeded 16°C (night) or 22°C (day). Supplemental lighting was also provided for 12 hours daily to enhance photosynthetically active radiation.

Ecological field data

The ecological data for the first part of the thesis (**Chapter I**) was collected from the fields of the central highlands of Eritrea, where *O. ficus-indica* grows abundantly. The central highlands of Eritrea are characterized by elevations exceeding 1500 meters and a mean annual rainfall of approximately 500 mm. This region has a warm to cool semi-arid climate, with potential evapotranspiration ranging from 1300 to 1800 mm. The rainy season typically spans three months, from June to August with random showers that occur in March and April (Ogbazghi and Stillhardt 2011). The area primarily falls within the Afromontane regional centre of endemism (White 1983), characterized by dry vegetation. **Chapter I** aimed to analyse the ecological impacts of *O. ficus-indica* by selecting diverse representative habitats in the central highlands of Eritrea (Fig. 2). The chosen habitats were intended to offer a comprehensive view of the invasive success and its effects, focusing on contrasting environments of a relatively humid site, rocky drier site, and a site with minimal human interference. This selection allowed for an assessment of invasive success and its influence on the Eritrean highlands. At each site, comparisons were made between areas invaded by *O. ficus-indica* and adjacent uninvaded areas with similar site conditions (5–10 m distance from invaded plots). A total of 36 pairs of plots, each measuring 10 x 10 m, were sampled, with 12 pairs at each site. These pairs represented the invaded (*O. ficus-indica*) and non-invaded (control) groups. Within each plot, the composition and cover of understory

vegetation, shrub layer, and tree layer were recorded and estimated. The objective was to analyse species composition and compare species richness and diversity between *O. ficus-indica* invaded and uninvaded plots.
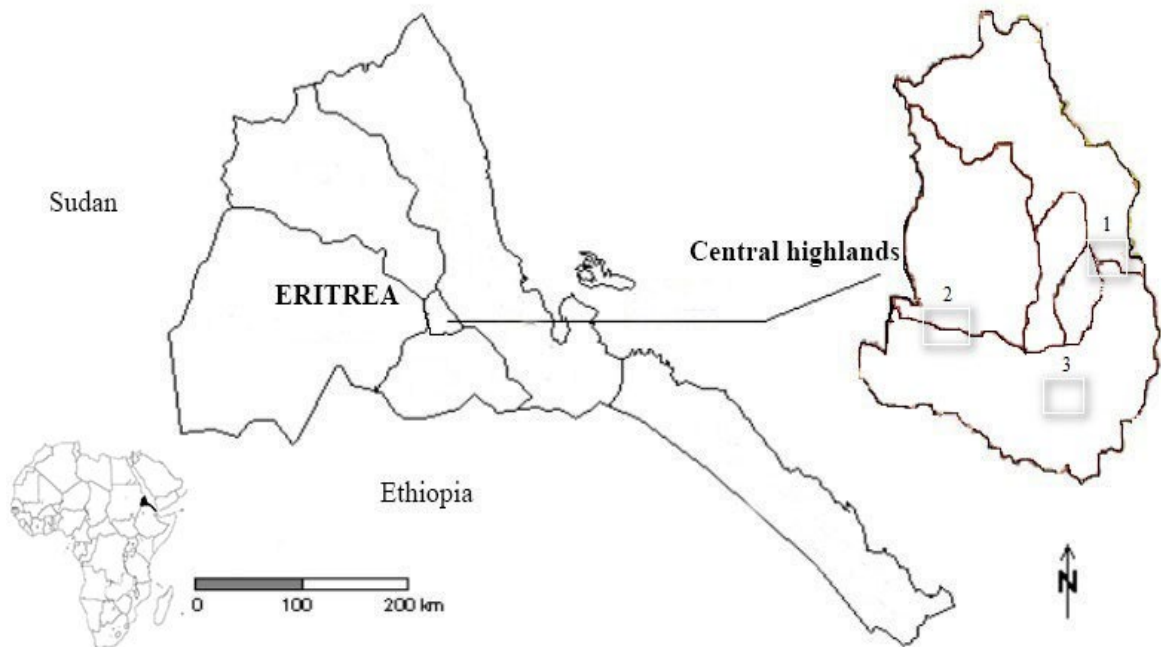

Fig. 2 Map of the three sites in the central highlands of Eritrea where the ecological field data was collected.

Competition experiment

In **Chapter II**, a common-garden pairwise competition experiment was conducted in Greifswald, Germany, from February 2020 to May 2021, where two species native to the highlands of Eritrea, *Ricinus communis* and *Solanum marginatum*, were selected to assess the competitive potential of the invasive cactus, *Opuntia ficus-indica* (Fig. 3). Two resource availability (water) treatments were established, representing dry and wet environments. Each treatment comprised fifty pots of one litre in size with a substrate mix of 75% loamy forest soil and 25% quartz sand. Plants were categorized into intraspecific monocultures for each species and interspecific polycultures. In the intraspecific category, each pot contained a pair of *R. communis*, *S. marginatum*, or *O. ficus-indica* plants. The interspecific category comprised pots with *O. ficus-indica* and either *R. communis* or *S. marginatum* pairs. Half of the pots for each category were allocated to wet and dry conditions.
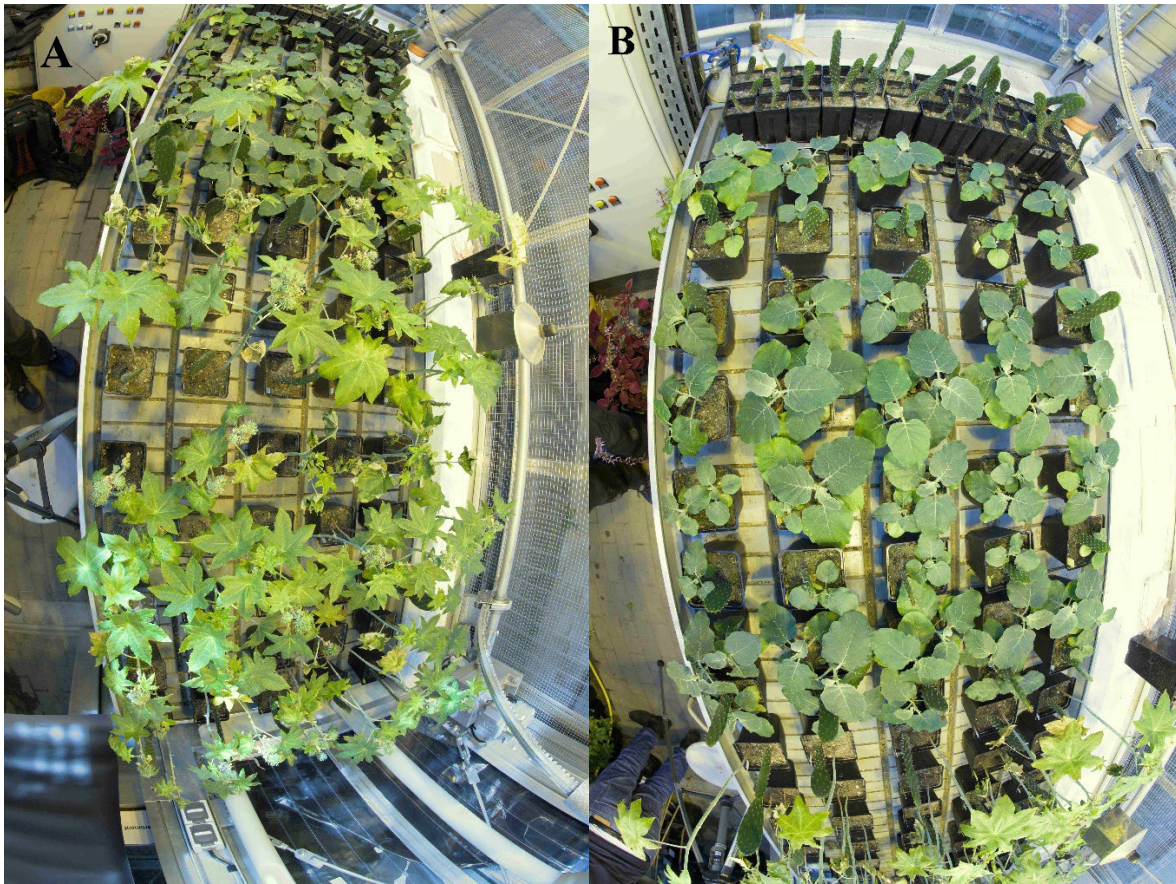
Fig. 3. Competition experiment between *Ricinus communis* (a) and *Solanum marginatum* (b) with *Opuntia ficus-indica* respectively, in the greenhouse of the Greifswald Botanical Garden.

Pretrial on the tolerance limits of *Opuntia ficus-indica*

The invader, *Opuntia ficus-indica*, displayed remarkable resilience, surviving nine months without watering. An additional pretrial experiment assessed water tolerance, exposing 16 plants to varying water availability (0 to 260 ml of water per week) over nine months (Fig. 4). Despite growth impediments at lower water levels, all plants survived, even without water for nine months. A subsequent recovery experiment demonstrated rapid recovery within five days for plants previously exposed to drought. Notably, a plant submerged in a bucket of water for three months, receiving the highest water amount, showed no signs of stress, emphasizing its resilience.
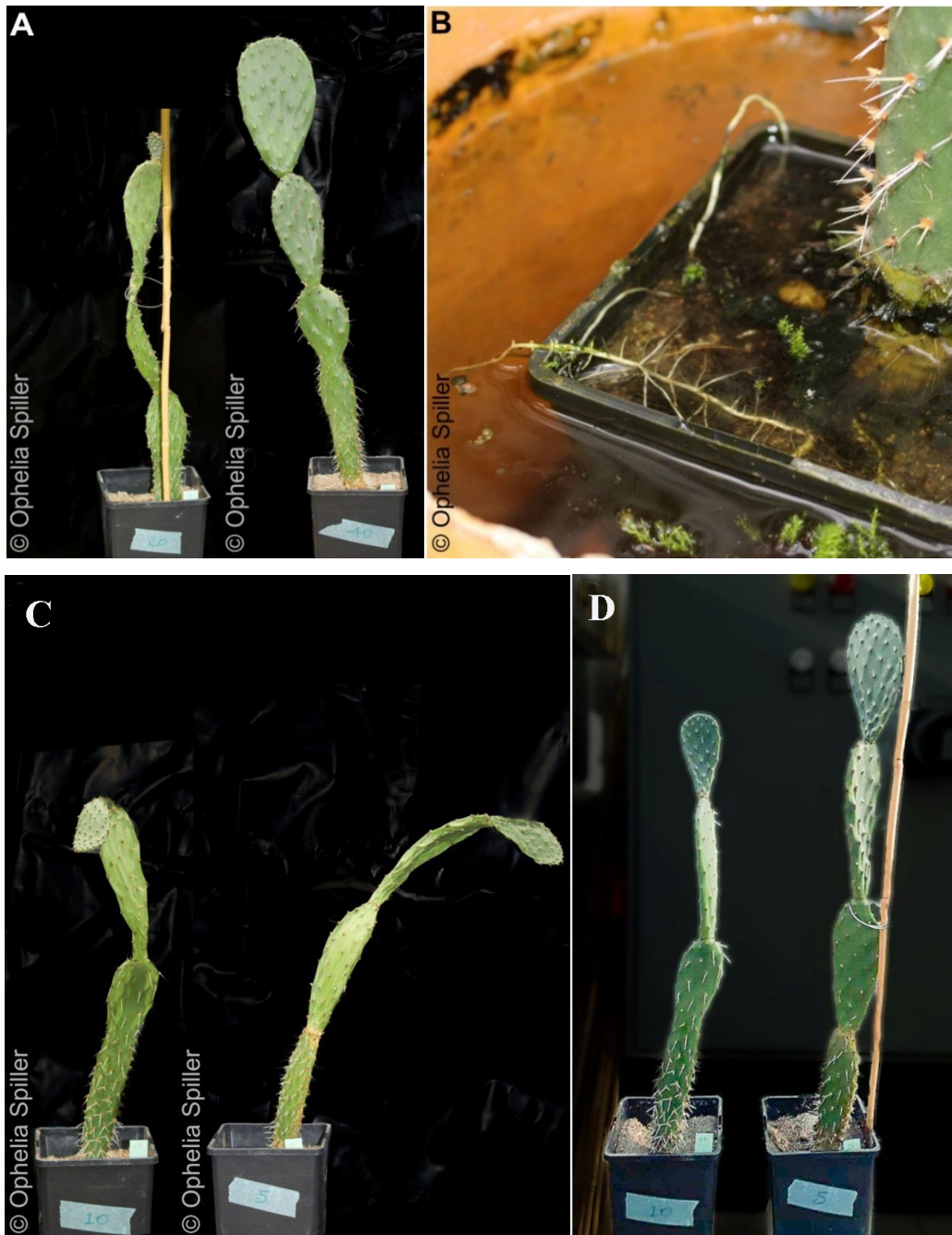
Fig. 4. Visual observations at the end of the drought pretrial experiment (a) Left: The plant was provided with 20 ml of water twice a week, right: 40 ml twice a week. (b) Close-up photo of the plant that was provided with the highest amount of water throughout the experiment (260 ml twice a week) and later submerged in a bucket full of water for three months. Surprisingly, roots are seen to grow outward on the surface of the water, probably seeking oxygen access. (c) Left: The plant was provided only with 10 ml of water twice a week, right: only 5 ml twice a week. (d) The same plants from (c) in a recovery experiment were provided with 100 ml water twice a week. Visual observations within five days of the recovery experiment.

Provenance trials

Similarly, in **Chapter III,** a common-garden drought experiment was conducted from September 2020 to November 2022 in Greifswald, Germany, aimed to assess the plasticity of *Opuntia ficus-indica* in response to different water availability levels. Seeds from 12 populations of *O. ficus-indica* were planted, comprising three from its native region in Mexico (Jalisco), three from various locations in Africa (Algeria, Eritrea, Ethiopia), one from Madeira Island off Africa's coast, and five from Europe (Italy and Portugal), capturing diverse genotypes (Fig. 5). Plasticity was evaluated under two water availability conditions, simulating dry and wet environments. From a total of 120 pots, each population's plants (n = 10) were randomly assigned to two water availability treatments: a "wet" treatment receiving 160 mL of water twice weekly and a "dry" treatment receiving 40 mL of water twice weekly. The watering regimens were determined through the pretrial experiment.

Fig. 5. *Opuntia ficus-indica* from all the provenances (12 populations) growing in the greenhouse of the Greifswald Botanical Garden.

Synopsis

Invasive plants possess a set of characteristics that enable them to become successful invaders in their introduced ranges. One key factor is their rapid growth and high reproductive capacity, allowing them to establish and spread quickly in the new environment (Richardson and Rejmánek 2011). Additionally, the absence of natural predators, herbivores, or pathogens in the introduced range, which typically controls their populations in their native habitats, might give invasive plants a competitive edge (Keane 2002). This enemy release hypothesis is one of the widely proposed explanations for the success of invasive species (Colautti and MacIsaac 2004; Middleton 2019). Additionally, it plays an important role in shaping the development of biocontrol programs designed to mitigate the impact of invasive species. In contrast to Eritrea's experience, numerous other countries have made attempts to employ biological control measures against the invasion of *Opuntia ficus-indica* (Hoffmann et al. 2020; Humphries et al. 2022; Zimmermann and Moran 1991). The lack of enemies carries particular significance during the initial introduction of invasive species, but the invasive species employ multiple mechanisms to establish themselves.

Invasive species are highly efficient in utilizing available resources like water, nutrients, and sunlight, making them better adapted to the new ranges (Daehler 2003). Their ability to flower early and produce more seeds or vegetatively grow for an extended period increases their chances of successful establishment by creating a substantial seed bank (Baker 1974), as commonly observed in *O. ficus-indica* (**Chapter I**). Moreover, mechanisms for long-distance seed dispersal, such as wind, water, or animal dispersion help invasive plants colonize new areas effectively (Nathan et al. 2011). The dispersal mechanisms in invasive species such as *O. ficus-indica*, as it produces edible fruits as well as cladodes which can be consumed by humans and animals, can further enhance its spread.

Human activities and disturbances play a significant role in the success of invasive plants. These disturbances, often caused by human actions such as habitat destruction, land use changes, and pollution, create open niches that invasive plants exploit to establish and dominate (Hobbs and Huenneke 1992). Similarly, in the Eritrean highlands, *O. ficus-indica* has been extensively planted in hills and mountains to prevent erosion and for soil conservation (Bein et al. 1996). Additional practices of fruit harvesting for consumption and commercial purposes have contributed to its further spread in these areas. Moreover, the cutting of the cladodes to clear land passages also provides benefits to *O. ficus-indica*, as it promotes vegetative growth from fallen cladodes on the ground (**Chapter I**). The ecological

effects of these spread of *O. ficus-indica* in the field was identified using the mechanism of space for time substitution as *O. ficus-indica* has already been growing in the study site for over a century. This method has some limitations as it assumes that the processes driving changes over time are the same as those driving differences across space, which may not always be the case. For instance, the time gap that exists between the establishment of invasive species and the increased negative effects on the native species provides a valuable window of opportunity for native species to evolve adaptive traits, thereby enhancing their chances of survival within the newly restructured ecological community (Stotz et al. 2016). This evolutionary response might not be captured in a space-for-time substitution study. It is beneficial to have continuous monitoring of the development of invasive species as soon as they have been identified. This is usually difficult, as the identification of the invasive species during the time of introduction and establishment may not occur. However, after the species is identified for its potential effects, monitoring the development of the spread would give additional information in understanding the effects of invasive species. Therefore, while the space-for-time substitution mechanism can provide valuable insights into the dynamics of plant invasions, it should be complemented with additional field research and approaches to provide a more comprehensive understanding of plant invasions.

Why is *Opuntia ficus-indica* a successful Invader?

Invasive plants frequently exhibit increased growth and survival rates resulting from vegetative propagation compared to those from sexual reproduction. Several invasive species use this strategy, e.g., *Phragmites australis* (Albert et al. 2015), *Fallopia japonica* (Forman and Kesseli 2003) and *Opuntia ficus-indica* (**Chapter I**). This is attributed to their status as clones of the parent plant, giving adaptation to the local environment. The ability for high seed production or extensive vegetative propagation and growth, seen in *O. ficus-indica*, proves advantageous in its invasion success (**Chapter I**) even though its competitive ability is not as strong (**Chapter II**) as most other invasive species (Gioria et al. 2023). Invasive plants utilizing vegetative reproduction can sustain significant biomass and reproductive output throughout their invaded range. This is often characterised by fast growth within the invaded territory, resulting in higher vegetative biomass and reproductive output (**Chapter II**; Helsen et al. 2020). These can cause pressure on the diversity and richness of the native plant community which might result in the loss of biodiversity or the homogenization of the invaded plant communities (**Chapter I**). These pressures on the native communities are usually determined by the space-for-time substitution mechanism

(Thomaz et al. 2012). This method is useful when there is no long-term data on the ecological sites and the mechanism of space for time assumes that the temporal changes can be used to represent the spatial differences. i.e., for example, when comparing the differences between the *O. ficus-indica* invaded and non-invaded sites.

These negative impacts on the native plant communities might be, as mostly seen in several invasive plants, the competitive abilities of the invader (Čuda et al. 2015; Levine et al. 2003; Vilà and Weiner 2004). On the contrary, like some invasive species, *Opuntia ficus-indica* showed weaker competitive abilities (**Chapter II**; Franzese and Ghermandi 2014; MacDougall and Turkington 2005). This indicates that it uses other strategies to outgrow the native species and eventually cause negative effects, such as the homogenization of the native community (**Chapter I**). The special trait of displaying the capacity for vegetative reproduction achieves most of its successful spread through a combination of other factors, including higher biomass production and drought tolerance. These traits, which might also be referred to as novel weapons (Callaway and Ridenour 2004), enable the fast establishment of the invader in new areas, taking advantage of native species, and the maintenance of high fitness in novel environments.

Drought resistance

Invasive plant species with drought tolerance possess an advantage in colonizing and dominating new environments, primarily due to their ability to thrive under water-limited conditions. This advantage stems from their reduced competition with native plants during droughts, rapid establishment, increased reproductive success through drought-adapted strategies, and adaptability to varying environmental conditions (Funk 2013). *Opuntia ficus-indica* as a drought-tolerant invasive cactus utilizes these traits to overcome its weakness in being a successful competitor (**Chapter II**). Similar patterns of drought tolerance are also observed in other invasive species such as Tamarix spp. (Lee 2022), *Bromus tectorum* (Zelikova et al. 2013), and *Elaeagnus angustifolia* (Collette and Pither 2015). The ability of stress tolerance, where species can withstand and cope with various abiotic and biotic stress factors, such as drought, temperature extremes, or competition for resources (Yin et al. 2023), plays an important role in the invasion success. As a result, this tolerance gives *O. ficus-indica* the potential to further affect the growth balances, particularly in resource-limited ecosystems such as the water-limited arid/ semi-arid subtropical shrublands. In the context of plant competition, water availability plays an important role in affecting the level of competition and the mechanisms plants use to compete for resources (Craine and

Dybzinski 2013). For instance, the limitation of available water may cause plants to increase their root growth to access more water, which can eventually intensify competition for water and nutrients in the soil (Foxx and Fort 2019). Additionally, water stress can impair plant growth and increase the proportion of visibly wilted leaves, affecting the overall health and competitive ability of the plants (Chen et al. 2022). The highly water-efficient CAM (Crassulacean Acid Metabolism) photosynthetic strategy available in species like *O. ficus-indica* (*Chapter II*) and *Cylindropuntia rosea* (Masrahi et al. 2022) could benefit invasive species as a so-called 'novel weapon' (Nobel 2002) in dry environments and the ongoing climate change causing water scarcity leading to drought.

Climate change can have a significant impact on the spread and impact of invasive plant species. As the climate changes, new conditions are encountered by both native and invasive species with fluctuations in temperature and rainfall (Dai et al. 2022). The ongoing warming caused by climate change can accelerate and intensify the impacts of invasive species, and disrupt and impede the ability of native species to adapt to climatic conditions that are beyond the usual frequency and magnitude (Leal Filho et al. 2018). The invasion success of *Opuntia ficus-indica* will be amplified with these climatic changes that are particularly pronounced in the regions of the subtropical arid/semi-arid drylands (Funk et al. 2015; Serdeczny et al. 2017). In addition, climate change can lead to increased disturbance, and invasive species generally thrive in disturbed communities where on the other hand, native species may decrease in abundance, and diversity and change their community composition (**Chapter I**; Kneitel and Perrault 2006). Disturbance in the native vegetation due to drought might therefore create gaps with little to no interspecific competition for *O. ficus-indica* enabling it to spread rapidly. Moreover, within the dry ecosystems, water availability becomes a major source of competition, favouring plants like *O. ficus-indica* which can endure water shortages, but readily take up large amounts of water as soon as it becomes available with its rapidly forming rain roots and storage in its succulent tissue. Invasive species can adapt to these rapid climate-induced environmental changes using phenotypic plastic responses. Phenotypic plasticity can allow invasive species, like *O. ficus-indica*, to rapidly adapt to these changing conditions, which may further enhance their invasiveness (Bonamour et al. 2019; Fox et al. 2019; Levine et al. 2003). The adaptation and plastic responses of *O. ficus-indica* have contributed to its success in various environmental conditions of the different regions of the world that it has invaded (**Chapter III**).

The role of phenotypic plasticity

Phenotypic plasticity, the ability of an organism to change its characteristics in response to changes in the environment, plays a significant role in the success of invasive species, enabling them to adapt to diverse habitats and environmental circumstances. It is usually assumed that invasive species show increased plasticity in their introduced ranges compared to their native ranges (Parker et al. 2013). This higher phenotypic plasticity contributes to the success of invasion by introduced plant species allowing them to adapt to various environments, that further facilitate their spread and establishment (**Chapter III**; Richards et al. 2006; Sexton et al. 2002). Similarly, *Opuntia ficus-indica* showed generally improved performance in its introduced ranges than the native range, showing its successful spread.

Phenotypic plasticity plays an important role in the success of *Opuntia ficus-indica* in the introduced environments. In the invasive populations, *O. ficus-indica* displayed a higher level of adaptability to changing water availability compared to the native populations (**Chapter III**). This increased adaptability, combined with its ability to withstand drought, and exhibit rapid growth in response to water availability, makes it exceptionally well-suited for invading regions with highly variable water conditions, including extended dry periods. Therefore, *O. ficus-indica* is likely to benefit from climate change, particularly as climate change leads to more frequent water availability fluctuations, potentially accelerating its spread in native plant communities across arid, semi-arid, Mediterranean, and subhumid ecosystems. Climate change, through the expansion of arid areas and desertification, is expected to amplify the invasion success of this species. As climate change expands arid areas, species like *O. ficus-indica* which are highly plastic and adapt to diverse environments, survive dry spells, and grow rapidly in times of high-water supply, are likely to increase their invasion potential.

Conclusions and perspectives

This PhD thesis investigated the ecological impacts of *Opuntia ficus-indica* invasion within a specific region characterized by similar climatic conditions. The primary focus of the initial study was on a specific feature of ecosystem properties, namely the spatial diversity of native species. Broadening the scope of the research to encompass various ecosystem properties across diverse regions could enhance our comprehension of the broader impacts of *O. ficus-indica* beyond the already identified effect on spatial diversity. This investigation could be complemented by additional field competition experiments, incorporating mechanisms such as competitive exclusion and competitive release (Segre et al. 2016) that consider additional

factors like grazing and disturbance that have notable impacts on ecosystem services. Adopting these approaches would facilitate the discovery of additional native species that coexist and exert influence on the competitive abilities of *O. ficus-indica*.

One crucial factor that contributes to the successful expansion of invasive species into new habitats lies in their superior competitive abilities relative to native species. However, our competition experiment revealed an interesting exception: *Opuntia ficus-indica*, unlike most invasive species, proved to be an inferior competitor. This finding challenged our initial hypothesis and expectations regarding its negative ecological impact on native communities. Recognizing the need for an alternative explanation for its successful invasion despite lacking competitive ability, we observed that *O. ficus-indica* demonstrated significantly higher growth, even under competitive pressures, compared to native species. This higher growth potentially strengthened its dominance over native plant communities, primarily attributed to its unique vegetative growth characteristics that facilitated rapid expansion. Additionally, the species exhibited homogenizing effects in native plant communities by displacing native species and permitting only specific ones to thrive in its proximity. In our study, we adopted a simple additive design (Freckleton and Watkinson 2000) for the competition experiment planting species in pairs to investigate their interactive effects. This design allowed us to assess the additive impacts of each species on one another, providing insights into how *O. ficus-indica* influences the growth and interactions of native species. While this approach offers valuable information, a more comprehensive future exploration could involve comparing *O. ficus-indica* in a full additive design with native species identified through field experiments. The full additive design, encompassing all possible species combinations, would enable a thorough examination of interactive effects in diverse scenarios. Careful selection of native species, emphasizing those with similar growth forms and life strategies, is pivotal for obtaining accurate insights into species interactions.

Comparing populations in different introduced or invasive ranges with those in the native range offers an additional perspective on the extent of spread and the mechanisms facilitating the success of invasive species. Examining differences between native and invasive ranges can reveal how plastic the species become over time. Therefore, understanding the role of phenotypic plasticity in the success of invasive species in both arid and less arid environments is crucial for predicting and managing the impacts of climate change on biodiversity and ecosystem functions. The higher the observed phenotypic plasticity, the greater the potential to overcome challenges arising from novel environments with varying

climatic conditions. A common approach to assessing the phenotypic plasticity of *Opuntia ficus-indica* involved conducting a common garden experiment, subjecting populations from different invasive ranges and the native range to wet and dry treatments. This approach, incorporating both native and invasive ranges, facilitates a comparative analysis of how environmental conditions influence phenotypic expression. Future implementations could benefit from reciprocal transplant experiments (Cui et al. 2018; Williams et al. 2008), enabling a more direct examination of local adaptation and phenotypic responses to diverse conditions, thereby enhancing our understanding of the effects of phenotypic plasticity. Additionally, incorporating gradient studies along introduced ranges may shed light on the gradient-dependent nature of plastic responses (Arnold et al. 2022; Valladares et al. 2006). Integrating these approaches enables a comprehensive evaluation of *O. ficus-indica*'s phenotypic plasticity and contributes to a better understanding of its adaptive strategies in diverse environmental conditions across native and introduced ranges.

Climate change-induced droughts occur with increased intensity and frequency in arid and semi-arid regions, creating favourable conditions for the thriving of drought-tolerant invasive species like *Opuntia ficus-indica*. These ecosystems, already under water stress, are particularly susceptible to the intrusion of invasive species. The impact of climate change is further exacerbated as it diminishes native ecosystem resilience and disrupts biodiversity. The higher occurrence of extreme weather events, characterized by reduced rainfall and frequent droughts, places additional stress on native species while concurrently providing opportunities for the increased spread of invasive species. Therefore, a comprehensive understanding of the tolerance limits of *O. ficus-indica* across its various introduced populations with diverse climatic conditions is essential for predicting its future spread and assessing potential impacts.

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Chapter I: The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea.

Yohannes B. Tesfay and Juergen Kreyling

ORIGINAL PAPER

The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea

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Abstract Invasion by exotic species is recognized as one of the major threats to biodiversity. The effects of invasion by *Opuntia ficus-indica* (Cactaceae) on the species diversity, richness and composition of invaded communities were studied at three sites in the highlands of Eritrea, East Africa. This paper investigates whether the presence of *O. ficus-indica* causes a negative effect on the native biodiversity in a region rarely studied so far. The vegetation in invaded and uninvaded plots with similar habitat conditions was sampled and differences in the species composition, diversity and richness were compared between the plots. The overall plant species composition differed significantly with invasion by *O. ficus-indica*. The invasion by *O. ficus-indica* also led to a significant homogenization of community compositions. The species richness and Shannon diversity index did not differ significantly between the invaded and uninvaded plots. Nevertheless, we still detected species with significantly lower occurrence in the invaded plots (*Psiadia punctulata*), but also species which preferred invaded plots (*Plectranthus hadiensis*). We conclude that *O. ficus-indica* exerts a negligible effect on the species diversity and richness but that it affects species composition and that there are species which suffer due to its presence. Due to the continuous pressure of the invasion by *O. ficus-indica* on the species composition and dry climates, further homogenization in the native species diversity is to be expected in the future for the highlands of Eritrea.

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Introduction

Invasion by introduced exotic species is recognized as one of the major environmental problems and threats to biodiversity (Di Castri et al. 1989; Di Castri and Hansen 1990; Williamson 1996). Many of the deliberate introductions relate to the human interest in nurturing species for agricultural, forestry or ornamental uses (Staples 2001). Invasion by exotic plant species can significantly alter the native plant community composition and ecosystem processes (Vilà et al. 2011), although the types and magnitudes of

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impacts of individual invasive species can vary with the type of ecosystem or invasive species (Fridley et al. 2007; Stohlgren and Rejmànek 2014). Even though some studies argue that plant invasions rarely cause biodiversity loss (Sax et al. 2002; Gurevitch and Padilla 2004; Maskell et al. 2006; Stohlgren et al. 2008), others have shown significant declines in biodiversity due to introduced invasive plants (Wilcove et al. 1998; Pimentel et al. 2001; Pauchard and Shea 2006). Various invasive plants are also known to change species composition or diversity (Vilà et al. 2006; Gaertner et al. 2009; Hejda et al. 2009; Powell et al. 2011), decrease ecosystem productivity and alter the rate of nutrient cycling (Liao et al. 2008; Ehrenfeld 2003), and hence impact ecosystem services and human well-being (Pejchar and Mooney 2009). Moreover, invasive species have been considered important agents in homogenizing plant communities at spatially different levels (Dar and Reshi 2015; Lososová et al. 2016; Price et al. 2018). Biotic homogenization is the process of increasing similarity among previously distinct communities within a specific region (Olden and Rooney 2006; Smart et al. 2006) and plant invasions may cause homogenization of the natural habitats by adapting to the new environmental conditions and dominating the native vegetation (Van Kleunen et al. 2010; Sol et al. 2012; Morri et al. 2019).

Invasiveness is influenced by species traits and describes the extent to which an alien species can overcome biotic and abiotic barriers to establishment and spread in a new environment (Richardson and Pyšek 2006; Wilson et al. 2007). Invasive plants are successful due to several reasons. They can produce many viable seeds, be unpalatable to herbivores, easily establish in different environments, tolerate highly stressful conditions and/or have an ability to readily regenerate from seeds, stems or roots. These features enable them to survive, spread and ultimately impact the native ecosystem (Obiri 2011). *Opuntia ficus-indica* (prickly pear), native to Mexico, is an exceptionally successful drought-tolerant invasive cactus that grows in arid and semi-arid areas. *Opuntia ficus-indica* is considered as an ecosystem engineer as it modifies the habitats of the indigenous plant species and dependent animals (Jones et al. 1994). This species impedes the movement of livestock and humans as it forms impenetrable thickets. It displaces native plants and reduces the carrying capacity of pasture and particularly threatens large-scale cattle

ranching (Obiri 2011). *Opuntia ficus-indica* occurs in countries where it has been cultivated and is invasive in Australia, Eritrea, Ethiopia, South Africa, Hawaii, USA and also to some extent in Somalia and Yemen (Brutsch and Zimmermann 1995), as well as in the tropical forests and rangelands of Kenya and Tanzania (Obiri 2011, Oduor et al. 2018). Additionally, Novoa et al. (2015) report that *O. ficus-indica* is the most widespread invasive cactus distributed outside the native range in 22 different countries.

In Eritrea, *O. ficus-indica* is highly invasive and abundant with an estimated cover of about 10,000 ha in the highlands, especially on the eastern escarpments (Bein et al. 1996). There is no clear evidence as to when *O. ficus-indica* was introduced into Eritrea, but it is assumed to have been planted in the southern parts of the highlands as early as 1839 and was then brought to the central highlands (NEMP-E 1995). The fruit of *O. ficus-indica* is popular as food for humans as well as animals. Outweighing its benefits, *O. ficus-indica* is invading the highlands, potentially causing changes in the ecological functioning of the native Afromontane forests, which, according to White (1983), is one of the major regional centres of endemism. The Invasive Woody Plant Database comprises over 5000 publications on species invasiveness, whereby only 6% refer to tropical Africa (Obiri 2011). This implies that the pressure on the native diversity in the region has rarely been studied and we are unaware of any comparable studies in Eritrea.

This paper analyses the ecological impacts of *O. ficus-indica* on the native plant diversity in Eritrea. We hypothesized that the spread of *O. ficus-indica* affects the composition, diversity and richness of the native plant species. Additionally, we measured environmental factors that potentially influence the invasion of the plant. We hypothesized that *O. ficus-indica* thrives in higher elevations, steep slopes and shallow soil depths. This was mainly because *O. ficus-indica* has been planted in Eritrea for soil conservation and to prevent erosion at steep slopes and higher altitudes (Bein et al. 1996). All these assumptions were tested using original field data, based on the comparisons of vegetation with and without *O. ficus-indica*.

Materials and methods

Study species

Opuntia ficus-indica is an evergreen perennial plant that can grow up to 5 m in height. The species has succulent stems that are formed as a sequence of flattened segments, the cladodes, which generally have an elliptical base that supports the greatly enlarged, flattened upper portion. *Opuntia ficus-indica* has spines, morphologically corresponding to leaves. Its flowers (5–10 cm in diameter) are sessile and solitary, and the fruits are berries that are 4–8 cm in diameter (Gimeno and Vilà 2002) with an average of 273 seeds per fruit (Barbera et al. 1991). Nieddu and Chessa (1997) found the germination of the *O. ficus-indica* seeds reaching up to 90% in growth chambers with a day/night temperature of $30/20^0$C, but only reaching 55% when seeds were kept at room temperature and 43% when seeds were placed outdoors. The seeds are usually dispersed after consumption by humans, birds and other animals (endozoochory). Furthermore, vegetative propagation occurs through cladodes readily taking root upon falling to the ground and conspicuous patch formation is an important factor in the persistence of local populations of the plant, although seedling recruitment is essential for expanding the geographic range and establishment in new areas (Gimeno and Vilà 2002).

Study site

The study was conducted in the central highlands of Eritrea, where *O. ficus-indica* grows vigorously and is abundant. The central highlands lie at an altitude over 1500 m with a mean annual rainfall of 500 mm. It is an area with a warm to cool semi-arid climate and potential evapotranspiration ranging between 1300 and 1800 mm. In this area, the rainy season normally lasts about three months, beginning in June and ending in August. Besides heavy rain, occasional showers come in March and April (Ogbazghi and Stillhardt 2011). The vegetation map of Africa by White (1983) lists 20 major regional centres of endemism, of which four (the Sudanian, Somali-Massai, Afromontane, and Sahel regions) are well represented in Eritrea. The natural vegetation of the study site is the dry part of the Afromontane regional centre of endemism. The flora

as a whole is estimated to contain over 4000 taxa, of which 75% are likely to be endemic to the Afromontane regional centre (Ogbazghi and Stillhardt 2011). Despite this regional taxonomic richness, plot-level species richness is remarkably low, especially compared to the richness of higher taxonomic units (Hamilton 1976; Bekele 1994; Tura et al. 2017).

Sampling design

The ecological data were collected from June to August 2018. The fieldwork was conducted during and shortly after the rainy season for an effective sampling of the existing plant species because most of them sprout, leaf out and/or produce fruits during this time. Representative original habitats were selected at three different sites (Fig. 1) to identify and assess the ecological impacts of *O. ficus-indica*. The aim was selecting a wide range of habitats where *O. ficus-indica* has established sustained populations in the central highlands of Eritrea: (a) a relatively humid site in which *O. ficus-indica* was historically favoured by people for collection of fruits and free grazing takes place (site 1), (b) a rocky site and relatively dryer than the other two sites (site 2), and (c) a site protected from human use (site 3). This selection of contrasting sites provided a general picture of invasive success and its impact in the Eritrean highlands. At each site, we compared *O. ficus-indica* invaded areas with surrounding uninvaded areas, in which the uninvaded control plots were located as close to the invaded plots as possible to have similar site conditions (5–10 m distance). A total of 36 pairs of plots (12 pairs for each site and each plot measuring 10 × 10 m) were sampled to assess the potential effects of *O. ficus-indica* (Table 1). The pairs of plots represented the *O. ficus-indica* invaded group and the non-invaded or control group. In each of the plots, the floristic composition of the understory vegetation, the shrub layer and the tree layer were recorded and their covers estimated. The sampling approach was to examine species composition and to compare species richness and diversity estimates between *O. ficus-indica* invaded and uninvaded plots. Plant species were identified following Hedberg and Edwards (1989); Edwards et al. (1995); Edwards et al. (1997); Edwards et al. (2000); Hedberg et al. (2003); Hedberg et al. (2006); Mesfin (2004) and Bein et al. (1996). For
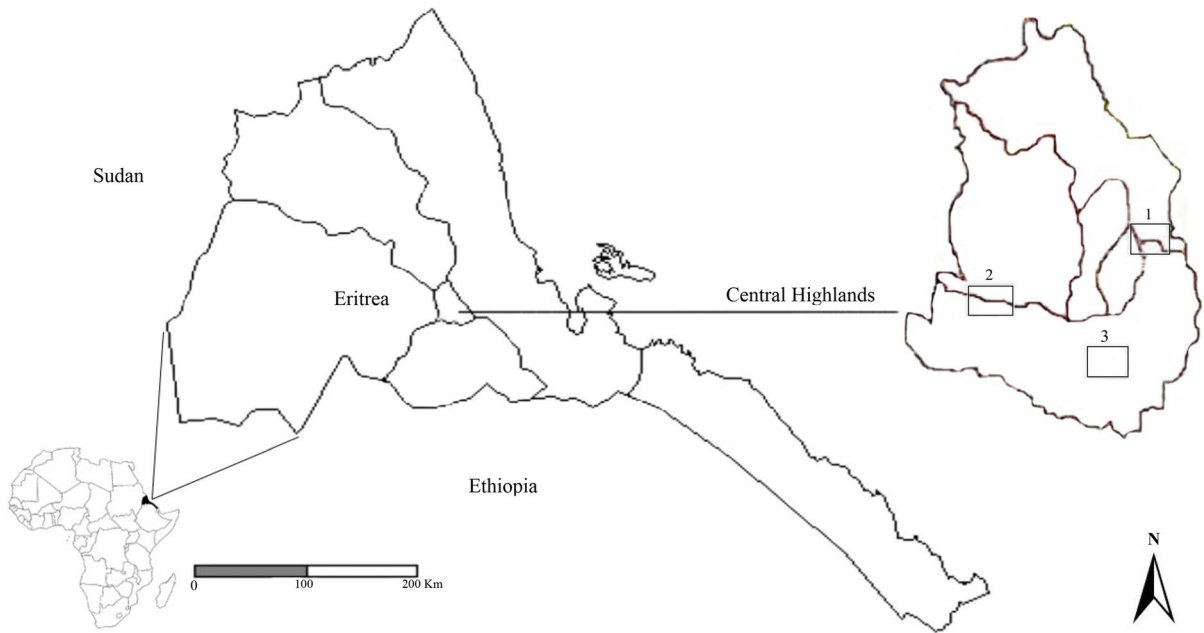
Fig. 1 A map of the study area and the three study sites in the highlands of Eritrea

Table 1 Basic geographical characteristics (average representation per site) of the three sites where the data were collected (Fig. 1). See Online Resource 1 for detailed information of each plot

Site	Position	Altitude (m a.s.l)	Slope (°)	Soil depth (cm)	Soil pH	No of plots
1	15.345N 38.962E	2395 ± 8	15 ± 2.8	12 ± 2.5	6.3 ± 0.4	24
2	15.248N 38.762E	2198 ± 6.6	8 ± 1.2	8 ± 1.2	6.4 ± 0.5	24
3	15.231N 38.899E	2245 ± 8	9 ± 2.9	12 ± 1.9	6.4 ± 0.4	24

accurate identification of some species, specimens were taken to the Herbarium of the Eritrea Institute of Technology. Additionally, environmental factors such as elevation in meters above sea level, soil pH measured in water, slope in degrees and soil depth in centimetres were measured. An average value of samples from three sides of each plot was taken to equally represent the environmental parameters.

Statistical analyses

We calculated differences in the composition of vascular plant species between the invaded and uninvaded plots of the three sites using an analysis of similarity (ANOSIM) with the function *anosim* in the vegan package (version 2.5-6; Oksanen et al. 2019). To assess the degree of similarity in community composition between plots, we computed the Bray–

Curtis dissimilarity index. This was performed based on the native species abundance. The values of Bray–Curtis dissimilarity index fall between 0, where the two communities are identical and 1, where the two communities are completely dissimilar and share no common species. Based on Bray–Curtis dissimilarity, we further tested for homogenization of the native plant communities by comparing the mean dissimilarity of invaded and non-invaded plots. Because of lack of independence in the data due to each plot being used for n-1 pairwise dissimilarity calculations, we tested for significance of differences in mean dissimilarity between the two groups by a permutation procedure which compared the observed difference in means to 1000 random draws (Jurasinski and Kreyling 2007). Then, non-metric multidimensional scaling (NMDS) (Kruskal 1964) was used to collapse the information of species compositions to two

dimensions for better visualization and interpretation. Additionally, the significant environmental vectors (elevation, slope and soil depth) were fitted into the ordination space using the function *envfit* in the vegan package. Furthermore, species that were significantly affected in their occurrence by the presence of *O. ficus-indica* were identified with an indicator species analysis (Dufrêne and Legendre 1997) using the *indval* function in labdsv package (version 2.0–1; Roberts 2019). The presence or absence of *O. ficus-indica* was used to differentiate the invaded and control plots. Thus, we excluded *O. ficus-indica* while calculating community composition or species richness. We fitted a linear mixed-effects model and used ANOVA (lmerTest package, version 3.1-0; Kuznetsova et al. 2017) to assess the effects of *O. ficus-indica* on indices of species diversity in which the indices of diversity were treated as dependent variables while invasion status of a plot was treated as a fixed-effect independent variable. Plot pair was nested within the study site and treated as a random-effect independent variable. Native species richness and Shannon diversity index were calculated and compared between control and invaded plots in the same way. All statistical analyses were performed in R (version 3.6.0; R Core Team 2019).

Results

A total of 45 plant species were identified from 25 families on the 36 pairs of plots (see Online Resource 2). The dominant families were Asteraceae, Lamiaceae, Fabaceae and Solanaceae. In the invaded plots, *O. ficus-indica* reached an average cover of 49% $\pm$ 18% (SD). The number of juvenile *O. ficus-indica* increased with the number of adult *O. ficus-indica* ($p = 0.026$; $r^2 = 0.14$) and a total cover of *O. ficus-indica* ($p = 0.001$; $r^2 = 0.26$), indicating its potential to form dense and lasting thickets once established.

The overall plant species composition between the pairs of invaded and uninvaded plots of the sites differed significantly (ANOSIM: R = 0.24; $p < 0.001$, Fig. 2). The invasion by *O. ficus-indica* led to a significant homogenization of community compositions (Fig. 3, permutation test: F = 19.6, $p < 0.001$). The environmental parameters with significant ($p < 0.05$) link to the plant species composition, in addition to the described effect of invasion by

O. ficus-indica, were elevation, slope and soil depth of the plots (Fig. 3). This result corresponded well with univariate regressions showing higher cover by *O. ficus-indica* with increasing altitude ($p = 0.002$; $R^2 = 0.23$), increasing slope ($p = 0.050$; $R^2 = 0.11$) and increasing soil depth ($p = 0.005$; $R^2 = 0.21$). The indicator species analysis (see Online Resource 2) revealed that *Plectranthus hadiensis* ($p = 0.007$) occurred together with *O. ficus-indica* more often, while *Psiadia punctulata* occurred more often in the absence of *O. ficus-indica* ($p = 0.041$).

The indicator species analysis showed that *Bidens pilosa* ($p = 0.10$) and *Tagetes minuta* ($p = 0.22$), which are themselves invasive species, had no significant link to the plots invaded by *O. ficus-indica*. We also checked their role in homogenization of communities by comparing plots where they were present to plots where they were absent. The results based on the subset of sites where the species occurred, *Tagetus minuta* ($p = 0.501$) and *Bidens pilosa* ($p = 0.165$) did not exert a significant effect on homogenization.

The species richness ($p = 0.311$) and Shannon diversity index ($p = 0.098$) did not differ significantly between the invaded and uninvaded plots. Furthermore, species richness and Shannon diversity were not significantly related to the cover of *O. ficus-indica* ($p = 0.226$ and $p = 0.191$, respectively).

Discussion

Our results showed that species composition of the plant communities was significantly homogenized by the presence of *O. ficus-indica* while species richness and Shannon diversity were not significantly affected by the presence of *O. ficus-indica*. This suggests that the spread and abundance of *O. ficus-indica* reduce landscape-level heterogeneity or spatial diversity (Jurasinski and Kreyling 2007) of the native plant communities. This finding corresponds well with other studies which have shown homogenization of native plant communities due to invasive species (McKinney 2005; Olden and Rooney 2006; Pino et al. 2009; Qian and Ricklefs 2006). Chen et al. (2013), for example, found that *Solidago canadensis* invasions have resulted in community homogenization across diverse habitats and landscapes which were formerly dominated by different species. They concluded that the community patterns of sites invaded by *S. canadensis*
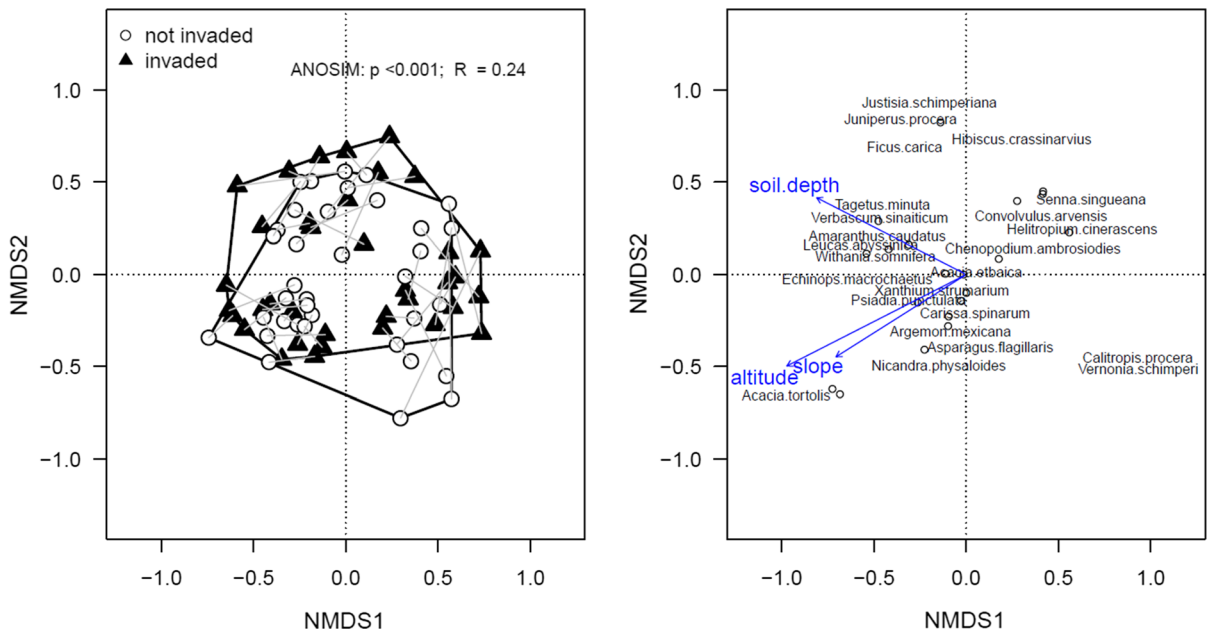
Fig. 2 The difference in species compositions between invaded and non-invaded plots graphically visualized by non-metric multidimensional scaling (NMDS). Statistics stem from an analysis of similarity (ANOSIM) based on Bray–Curtis

dissimilarity with final two-dimensional stress of 0.23. Species occurrence in the ordination and significant environmental parameters depicted in blue are shown for the same ordination in the second panel. See Online Resource 2 for the full species list
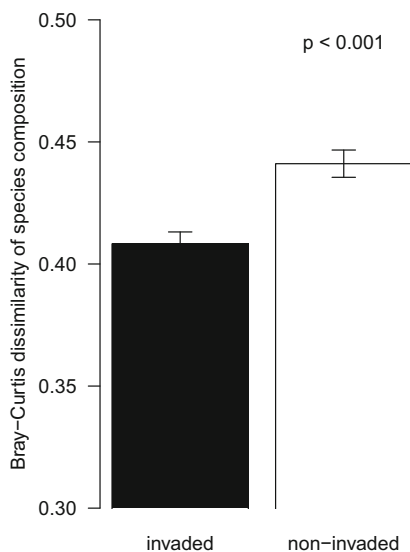

Fig. 3 Invasion by *O. ficus-indica* led to the homogenization of native plant community compositions as indicated by a decrease in mean Bray–Curtis dissimilarity. Displayed are the mean ± 1 SE of all pairwise Bray–Curtis dissimilarities per group. Significance of the differences between the invaded and adjacent uninvaded plots was tested using a permutation test with 1000 permutations

were highly similar to each other but dissimilar to those in the control sites, a scenario that corresponds to the homogenizing nature of invasive plants.

The ability to form homogenous stands, which is typical for *O. ficus-indica*, appears to drive the interference with the native species (Zimmermann et al. 2009). It has previously been reported that invasions can have a limited effect on species richness of communities (Hejda and Pyšek 2006). However, changes in species composition can occur and native, fast-growing species can increase in abundance in the invaded communities. Accordingly, we found *Plectranthus hadiensis*, a semi-succulent fast-growing herbaceous plant to occur more frequently with *O. ficus-indica*. On the other hand, *Psiadia punctulata*, a drought-resistant East African shrub was found to avoid the presence of the invasive plant. It is reported that *P. punctulata* is usually avoided by some herbivore animals even during severe drought conditions. An exudate, rich in pharmacologically active secondary metabolites, is potentially responsible for its unpalatable nature and drought resistance (Midiwo et al. 2003; Juma et al. 2001; Juma et al. 2006). We thus hypothesize that one important impact of the presence of *O. ficus-indica* on native diversity occurs

through affecting grazing and browsing patterns by herbivores. *Opuntia ficus-indica* likely shelters species sensitive to herbivory and competes with browsing-tolerant species for space, presumably explaining that its presence showed no significant impact on native species diversity and richness. These results imply that the impact of the invasive *O. ficus-indica* on the diversity and richness of native vegetation may be lower than previously thought. A similar situation was reported from Kenya (Oduor et al. 2018) where a similar study was performed by surveying the native vegetation in Nairobi National Park between *O. ficus-indica* invaded and uninvaded sites. They found that communities invaded by *O. ficus-indica* had significantly higher native species richness and diversity because *O. ficus-indica* sheltered the native species against grazing.

A potential drawback of observational studies comparing invaded and uninvaded habitats is that they may be biased by the fact that species diversity in itself can affect the likelihood of invasion, which makes it difficult to separate cause and effect (Hejda and Pyšek 2006; Levine and D'Antonio 1999; Hulme and Bremner 2006). However, since our results showed no difference in species diversity between invaded and uninvaded communities, the prediction that species-poor stands could have been more easily invaded is irrelevant to our study (Hejda and Pyšek 2006). Quantitatively measuring the impacts of invasive species on native communities in the field is difficult. This is because invasion is a long-term process rarely observed from the time of the introduction and establishment of the invasive species (Müllerová et al. 2005). We used the invaded and uninvaded plots to overcome this difficulty. The uninvaded plots represented the native vegetation before the invasion occurred (Pyšek and Pyšek 1995) which justifies the 'space for time' substitution approach that is often used in studies on vegetation succession (Alvarez and Cushman 2002; Badano and Pugnaire 2004; Ruprecht 2005). The measurements of the species diversity between the invaded and uninvaded plots were then used in quantitively assessing the species richness, diversity and composition of the vegetation.

In its regions of origin, *O. ficus-indica* is found at elevations of over 4700 m (Nobel 1994) or in the introduced areas such as South Africa and Australia in highlands above 2000 m (Johnson 1982;

Zimmermann and Moran 1991; van Sittert 2002). It is thus well-fitted to grow in high altitudes, and in our study area at the Eritrean highlands, it grows vigorously and is abundant at elevations around 2000 m. It is a common conception that *O. ficus-indica* is planted for soil conservation and prevents erosion at steep slopes and higher altitudes (Bein et al. 1996), and we thus expected to find it primarily in those habitats. With respect to the effect of the environmental parameters on invasibility, higher cover and invasion success occurred in steeper and higher sites than in flatter sites or at lower elevations. Erre et al. (2009) studied the distribution of *O. ficus-indica* in the Mediterranean Basin and on the contrary found that the invasive plant was not common at higher altitudes due to the low temperatures in the region. The cover of *O. ficus-indica* also tended to increase with increasing soil depth. This could be attributed to the government's efforts to prevent soil erosion by terracing the landscape in higher altitudes with steep slopes which eventually conserved the soil and resulted in higher soil depths.

The successful establishment of *O. ficus-indica* depends on its unique biological traits and the environmental characteristics of the ecosystems it invades. It is suggested that the fluctuation in resource availability makes plant communities susceptible to invasion (Davis et al. 2000). Water availability in dry climates displays an example for this theory, as temporal fluctuations cause intermittent lack of resource availability, followed by water availability upon rainfall. This pulsed regime of water availability can make communities vulnerable to drought-tolerant invasive specialists such as *O. ficus-indica*. Its invasion success may consequently be amplified by climate change, which leads to warmer and drier conditions in the study area (Funk et al. 2015; Serdeczny et al. 2017) and can be expected to further increase the competitive ability and thereby the invasiveness of *O. ficus-indica* as it originates from even warmer and drier conditions (Novoa et al. 2015). To better project the future invasive potential of *O. ficus-indica*, controlled competition experiments with *O. ficus-indica* and native plants are needed.

Our data show that invasion by *O. ficus-indica* leads to plant community homogenization in the Eritrean highlands. While species richness and diversity appear unaffected by this invasion, homogenization is another negative consequence. Successful recruitment and

densification of established *O. ficus-indica* stand suggest an intensification of this problem in future, likely exacerbated by climate change and further enhanced by the lack of awareness of the local communities on the impacts of its invasion (Ogbazghi and Stillhardt 2011). The nurturing of the plant for different local uses (e.g. hedging, fodder, edible fruits) utilizing its drought-tolerant nature increases the potential for further spreading of this invasive species (Bein et al. 1996) and the interference with the spatial diversity and ecosystem processes of the native vegetation. It will likely become a long-term dominant species with an increasing impact on the native vegetation. The real challenge now lies in raising the local awareness of the issue and preventing further spread of the species to other natural ecosystems.

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Chapter II: An inferior competitor is a successful invader due to its stress tolerance and productivity.

Yohannes B. Tesfay, Annika Blaschke and Juergen Kreyling.

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An inferior competitor is a successful invader due to its stress tolerance and productivity

Yohannes B. Tesfay✉, Annika Blaschke & Juergen Kreyling

The invasion of ecosystems by non-native species is recognized as one of the most significant global challenges, particularly in semiarid regions where native biodiversity is already under stress from drought and land degradation. The implicit assumption is that invaders are strong competitors, but a greenhouse pairwise experiment conducted to examine intraspecific and interspecific competition effects of *Opuntia ficus-indica*, a widespread invader in semiarid ecosystems, with two species native to the highlands of Eritrea, *Ricinus communis* and *Solanum marginatum*, revealed that *O. ficus-indica* is a weak competitor. The unique ability of *O. ficus-indica*'s fallen cladodes to undergo vegetative growth becomes a fundamental trait contributing to its spread. This growth strategy allows *O. ficus-indica* to outgrow native species and establish a significant presence. In direct interaction, the competition in aboveground productivity measured by the logarithmic response ratio for *O. ficus-indica* was 3.4-fold and 5.9-fold higher than for *R. communis* and *S. marginatum*, respectively. Belowground, the native *R. communis* was facilitated (− 1.00 ± 0.69) by *O. ficus-indica* which itself suffered from high competition. This pattern became even more evident under water shortage, where aboveground competition for *S. marginatum* decreased 5.7-fold, and for *O. ficus-indica*, it increased 1.4-fold. Despite being a poor competitor, *O. ficus-indica* outperformed *R. communis* and *S. marginatum* in both aboveground (4.3 and 3.8 times more) and belowground (27 and 2.8 times more) biomass production, respectively. The findings of this study challenge the common interpretation that invasive species are strong competitors and highlight the importance of considering other factors, such as productivity and tolerance limits when assessing the potential impacts of invasive species on semiarid ecosystems.

Invasive plants are often found to outcompete native species during their successful invasions of many ecosystems[1]. Thereby, invasive species can endanger populations of native species[2–4], reduce spatial diversity[5], or negatively affect crop yields[6]. All of these processes are commonly explained by the superior competitive abilities of the invasive species[7]. Moreover, the ability of the invasive species to adapt to a new environment can be influenced, either positively or negatively, by the presence of other species[8]. Some argue that only highly competitive species can spread in a new environment[9] after successfully overcoming biotic and abiotic barriers[10].

Field observations show that invasive species outcompete and limit the abundance of native species[7,11,12] and direct paired competition experiments generally support this finding[7]. Exceptions with highly competitive native species limiting the exotic invaders mainly stem from temperate grasslands[7]. Here, competition by native species has been shown to reduce invasive plant growth considerably and has an even stronger effect than herbivory. Accordingly, the high competitive abilities of native species can effectively reduce invasion[13–15]. Although some communities or ecosystems are more susceptible to invasions than others, there is limited understanding of the competitive balance between invaders and native species in subtropical semiarid shrublands[7], where unpredictable precipitation can cause strong abiotic stress as well as temporarily abundant available resources.

The susceptibility of communities to invasion is often increased by the presence of available resources due to fluctuating environments in time or disturbances in space[16,17]. The probability of an invasion occurring is closely linked to the resource availability during the invasion period, and this availability is, in turn, impacted by the degree of disturbance in that particular ecosystem[16]. Consequently, ecosystems in unpredictable climates where a limiting resource, here water, creates chronic stress but intermittent rainfall events causing unlimited availability at hardly predictable points in time, can be expected to offer little resistance to invasions. Subtropical semiarid drylands are such ecosystems, but little is known about invasion processes and competitive balances between invaders and native species in these ecosystems[7].

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Another factor that plays an important role in invasion success is stress tolerance, the ability of a species to withstand and cope with various abiotic and biotic stress factors, such as drought, temperature extremes, or competition for resources[18]. As a result, this tolerance has the potential to further affect the competitive balances, particularly in resource-limited ecosystems such as the water-limited semi-arid subtropical shrublands. In the context of plant competition, water availability plays an important role in affecting the level of competition and the mechanisms plants use to compete for resources[19]. For instance, limitation of available water may cause plants to increase their root growth to access more water, which can eventually intensify competition for water and nutrients in the soil[20]. Additionally, water stress can impair plant growth and increase the proportion of visibly wilted leaves, affecting the overall health and competitive ability of the plants[21,22]. The highly water-efficient CAM (Crassulacean Acid Metabolism) photosynthetic strategy could benefit invasive species in such an environment as a so-called 'novel weapon'[23,24].

Opuntia ficus-indica (prickly pear) is a cactus native to Mexico which is exceptionally successful in invading arid and semi-arid ecosystems, e.g., in Australia, South Africa, Kenya, Tanzania, Ethiopia, Eritrea, Somalia, Yemen, North America, and Hawaii[25–27]. Moreover, it is reported that *O. ficus-indica* is the most widespread invasive cactus, which has been found nowadays in 22 different countries on all continents except Antarctica outside its native range[28]. It is reported to alter the composition of the indigenous plant and animal communities[29] and to reduce spatial diversity[5]. Its invasion has economic effects by impeding the movement of livestock and humans, as it forms impenetrable thickets and thereby threatens large-scale cattle ranching[26]. The spiny nature of *O. ficus-indica* impedes browsing and grazing, and in heavily infested areas, livestock struggle to access grazing areas. This negatively impacts cattle ranching, reducing livestock numbers and harming the local economy[30,31]. Despite studies recognizing the utilization and grazing barriers of the cactus[32,33], we are unaware of clear data on the extent of the economic effects. Furthermore, *O. ficus-indica* capitalizes on its important high water use efficiency as a CAM plant. This adaptation not only grants drought tolerance but also empowers the plant to thrive in arid conditions, enabling survival with minimal precipitation[34,35].

Based on its invasion success, *O. ficus-indica* is assumed to outcompete the neighbouring native species[36] and, due to its strong drought tolerance[37,38], can become even more competitive when water availability is scarce. Coincidentally, projections of precipitation in vast parts of the areas invaded by *O. ficus-indica*, with ongoing climate change, will face increasing droughts in future, leading to water scarcity[39]. The competitive abilities of *O. ficus-indica*, however, have not yet been tested experimentally, neither under water-limited nor under wetter conditions.

Accordingly, this paper deals with pairwise competition experiments in two different water availabilities between the invasive plant *O. ficus-indica* and two typical and common native plant species of invaded areas in Eritrea, *Ricinus communis* and *Solanum marginatum*. Considering its global invasion success in dry ecosystems, we hypothesized that *O. ficus-indica* has a high competitive power and outcompetes the native species irrespective of water availability. We furthermore expected that its competitive superiority increases under water stress.

Materials and methods

Competitive balance between the invasive *O. ficus-indica* and two species native to the highlands of Eritrea, *Ricinus communis* and *Solanum marginatum*, was experimentally evaluated. All three species grow together in the highlands of Eritrea[5] at altitudes above 1500 m with a mean annual rainfall of 500 mm. It is an area with a warm to cool semiarid climate and potential evapotranspiration ranging between 1300 and 1800 mm. In this area, the rainy season normally lasts about three months, beginning in June and ending in August. Besides heavy rain, occasional showers come in March and April[5,46]. All three plant species/ seeds were collected from the highlands of Eritrea in 2018 with the permission obtained from the Ministry of Agriculture, Regulatory Services Department with a certificate issue number ER-PSC-00026. The species were identified following Hedberg and Edwards[47], Edwards et al.[48–50], Hedberg et al.[51,52] Mesfin[53], Bein et al.[54], and by comparing the collected specimens at the Herbarium of the Eritrea Institute of Technology. The plant collection and use were in accordance with all the relevant guidelines.

Study species

Vilà et al.[6] and Vilà and Weiner[7] criticise pairwise competition experiments between invasive and native species for selecting highly competitive and aggressive invaders and comparing them to rare and threatened native species, which, per se, are poor competitors. Here, we avoid this bias by comparing a globally successful invasive species to two common and widespread native species that overlap in range and are known to be tolerant to disturbance.

Opuntia ficus-indica (L.) Mill. (Cactaceae) is an evergreen perennial plant that can grow up to 5 m in height. The species has succulent stems that are formed as a sequence of flattened segments, the cladodes, which generally have elliptical bases that supports the greatly enlarged, flattened upper portions. *O. ficus-indica* has spines, morphologically corresponding to leaves. Its flowers (5–10 cm in diameter) are sessile and solitary, and the fruits are berries that are 4–8 cm in diameter[55,56]. Nieddu and Chessa[56] found the germination of *O. ficus-indica* seeds reaching up to 90% in growth chambers with a day/night temperature of 30/20 °C, but only reaching 55% when seeds were kept at room temperature and 43% when seeds were placed outdoors. The seeds are usually dispersed after the consumption of the fruits by humans, birds, and other animals (endozoochory). The seeds require comparatively long time for germination due to their hard, lignified integuments which need to be overcome by physical or chemical reactions[57]. Furthermore, vegetative propagation occurs through cladodes readily taking root upon falling to the ground and conspicuous patch formation is an important factor in the persistence of local populations of the plant, although seedling recruitment is essential for expanding the geographic range and establishment in new areas[55].

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Ricinus communis L. (Euphorbiaceae) is a fast-growing, soft woody shrub or small tree (up to 5 m tall) and utilizes the C3 photosynthetic pathway. *R. communis* is indigenous to eastern Africa, the south-eastern Mediterranean Basin, and India, and it is commonly distributed throughout the tropics and warm temperate regions. It has developed various strategies, such as rapid growth, allelopathy, thriving in a wide range of soil conditions, and high seed production, to adapt to the conditions of disturbed areas[58]. *R. communis* is also known as a poisonous plant due to the presence of toxic ricin and ricinine in its seeds and other parts, however, *R. communis* is still commonly used as an ornamental plant and for its antimicrobial features, it is used as a medicinal plant to treat several ailments[59].

Solanum marginatum L. (Solanaceae), native to the highlands of Eritrea and Ethiopia, is a perennial shrub that follows the C3 photosynthetic pathway. It can grow up to 2 m tall and its leaves are densely covered in white stellate hairs and armed on both the upper and lower surfaces with prickles[60]. In its native range, it usually occurs in disturbed areas between altitudes of 2000 m and 3000 m above sea level[61,62]. *S. marginatum* is usually unpalatable to herbivores mainly due to the presence of a poisonous alkaloid chemical compound[63,64].

These three species have all been referred to as weedy, thrive in disturbed areas[58,62,65], and possess chemical and/or physical defences against herbivory. They differ little in their potential plant heights, but in some morphological features; *O. ficus-indica*, as a cactus is a succulent plant that can store water, unlike the other two native species. Sharing a similar life strategy and avoiding the common bias of choosing rare native species[6,7] were the important considerations for choosing these two native species.

Experimental design

The competition between species can be quantified experimentally using indices based on pairwise experiments which express competition intensity, effects, and response[3,40]. Competition indices help to quantify the proportional decrease in native plant performance due to the competing effects of invasive species and compare the effects on different species or under different environmental conditions[40–43]. When interspecific competition is weaker than the intraspecific competition in an invaded ecosystem, each native species in that community limits its own population growth more than it limits that of the competitive invader[44,45].

The greenhouse competition experiment was carried out from February 2020 to May 2021 at Greifswald, Germany. Two species native to the highlands of Eritrea, *Ricinus communis* and *Solanum marginatum*, were selected to test the competitive potential of the invasive cactus, *O. ficus-indica* in a common-garden pairwise competition experiment. Two different treatments were set up based on resource availability (water), depicting dry and wet environments. Each treatment was prepared with fifty pots with a volume of one litre. The substrate was a mixture of 75% loamy forest soil and 25% quartz sand. All plants were raised from seeds. Since *O. ficus-indica* needed more time to germinate, it was sown in January 2019, eight months ahead of the other two plants, which were sown in August 2019. After being transplanted into their respective target pots on February 10th, 2020, all plants, regardless of the species, exhibited similar heights of approximately 15 cm and no conspicuous difference in belowground biomass (personal observation). The plants were categorized into monocultures of each species (intraspecific competition) and polycultures of each native together with the invasive (interspecific competition). The intraspecific category had a pair of *R. communis* plants per pot (20 replicates), a pair of *S. marginatum* plants per pot (20 replicates), and a pair of *O. ficus-indica* plants per pot (20 replicates). The interspecific category had *O. ficus-indica* and *R. communis* plants per pot (20 replicates) and *O. ficus-indica* and *S. marginatum* plants per pot (20 replicates). Half of the pots from each category were distributed to each condition of the wet and dry environment. The pots in the wet environment were watered twice per week with 100 ml of water, simulating a wet condition, the other half of the pots were watered only once per week with 100 ml. The watering regimes were based on pre-trials with all three species. The dry variant was set right above the limit at which the native species showed strongly increased mortality. The invader *O. ficus-indica* proved to be remarkably resilient, surviving for nine months without any watering. To assess the plant's water tolerance limits, we conducted a pot experiment, exposing 16 plants to a gradient of water availability ranging from no water up to 260 ml twice a week over a period of nine months. While the growth of the plants exposed to drought on the lower end of the gradient was impeded, all plants survived the experiment, even the one not receiving any water for 9 months. In a subsequent recovery experiment, the plants that were previously subjected to drought showed rapid recovery within 5 days. Additionally, the plant that received the highest amount of water was submerged in a bucket of water for three months and displayed no signs of stress; instead, its roots grew upward and out of the water (see Supplementary 1 online for details on the pretrial).

The effects of the invader in the main experiment were assessed by comparing the native species growing alone (intraspecific, i.e., the average of the two plants per pot) with those that were growing with the invader (interspecific) for the wet and dry treatment, respectively. The positions of the pots within the greenhouse were frequently interchanged to ensure similar environmental conditions and reduce edge effects of the glasshouse or general heterogeneity of environmental conditions. The plants were kept at an average of 40% humidity and in a 12-h day and night cycle, at temperatures of 20 °C and 12 °C, respectively.

Response parameters

We quantified above- and belowground net primary production at the end of the experiment (after 15 months of growth in competition), hereafter ANPP (Aboveground Net Primary Productivity) and BNPP (Belowground Net Primary Productivity). Belowground biomass was gently washed free from the substrate by rinsing it into a coarse sieve so that the substrate was washed away, and the roots and rootlets could all be collected. The above- and belowground biomasses were dried for five days at 60 °C and 100% ventilation and weighed.

Statistical analyses

The growth parameters (ANPP and BNPP) were analysed using a two-factorial analysis of variance (ANOVA[66]) with the explanatory factors being water regime (wet/dry) and competition (intraspecific/interspecific for both the native species and the invader, i.e., a factorial variable with four levels: native–native, native–invasive, invasive–native, and invasive–invasive, with the biomass value of the first named in each pair in interspecific competition and the average biomass of both individuals per pot in case of intraspecific competition) including their interaction. Single models were run for each native species (*S. marginatum* and *R. communis*) and each response parameter (ANPP and BNPP) for a total of four ANOVA analyses. Tukey's HSD post hoc tests[67] were used to assess the significance of differences in pairwise comparisons for significant interaction terms. Similarly, the same representation based on the total biomass production is also provided in the Supplementary 2 online.

Furthermore, two different competition indices were implemented; Logarithmic Response Ratio (lnRR) and Relative Neighbour Effect (RNE)[3,68,69]. As both indices yielded highly similar patterns, we present the results based on lnRR in the main text (Fig. 2) and based on RNE in the Supplementary 2 online.

The Logarithmic Response Ratio (lnRR) is computed by the natural log of the ratio between the mean value of the respective control treatment (intraspecific without a second species) and the value of each treatment growing in competition with a second species (interspecific). Smaller values indicate weaker competition with negative values showing facilitation, while larger values indicate intense competition between the species[3,43]. lnRR is expressed as:

$$lnRR = \ln\left(P_{contr}/P_{mix}\right)$$

where ln is the natural logarithm, P_{contr} is the performance of the plant growing in a monoculture and P_{mix} is the performance of a plant growing in a mixture.

The effect of the different water regimes on the competition index data was examined using a one-way analysis of variance with water regime (dry/wet) as explanatory factor. Single models were run for each native species (*S. marginatum* and *R. communis*) and each response parameter (ANPP and BNPP) for a total of four ANOVA analyses.

Parametric assumptions were checked for all ANOVA models by examining the diagnostic plots (residuals versus fitted plots for homoscedasticity of the residuals and normal qq-plots for normal distribution of residuals[70]. According to the diagnostic plots, the ANPP and BNPP for both the *R. communis* and the *S. marginatum* datasets were log(x + 1)-transformed. The competition index datasets did not require transformations. For graphical visualizations, the function bar graph.CI in the R package sciplot[71] was used. All statistical analyses were done in R version 4.2[72].

Results

ANPP of *O. ficus-indica* was 4.3-fold higher under intraspecific competition than when competing with *R. communis* (Fig. 1a). In comparison, the native *R. communis* was 14-fold less productive aboveground than *O. ficus-indica*, but its ANPP was unaffected by the identity of its neighbour as its production did not differ between intra- and interspecific competition. *O. ficus-indica* was unaffected by the water regime in ANPP while the native *R. communis* produced 2.2 times more aboveground biomass under wet conditions and intraspecific competition than under dry conditions and interspecific competition (Fig. 1a).

BNPP of *O. ficus-indica* was 27-fold higher under intraspecific competition than when competing with *R. communis* (Fig. 1b). In comparison, the native *R. communis* was 17-fold less productive belowground under intraspecific competition than *O. ficus-indica*, but its BNPP even increased 3.1 times under interspecific as compared to intraspecific competition. *O. ficus-indica* doubled its BNPP under the dry as compared to the wet water regime when growing with itself but produced very little BNPP and showed no water effect when grown under interspecific competition. *R. communis*, in contrast, increased its BNPP in dry conditions 1.9 times over wet conditions only when growing in interspecific competition with *O. ficus-indica*, but not when growing with itself (Fig. 1b).

ANPP of *O. ficus-indica* was 3.8-fold higher under intraspecific competition than when competing with *S. marginatum* (Fig. 1c). In comparison, the native *S. marginatum* was 11-fold less productive aboveground than *O. ficus-indica*, but its ANPP was unaffected by the identity of its neighbour as its production did not differ between intra- and interspecific competition. In interspecific competition with *S. marginatum*, *O. ficus-indica* increased its ANPP 1.7-fold under wet as compared to dry conditions, while it did not show an aboveground growth response to the water regime when growing with itself. The ANPP of the native *S. marginatum* was unaffected by the water regime, irrespective of competition (Fig. 1c).

BNPP of *O. ficus-indica* was 2.8-fold higher under intraspecific competition than when competing with *S. marginatum* (Fig. 1d). In comparison, the native *S. marginatum* was only half as productive belowground as *O. ficus-indica* under intraspecific competition but showed a pattern similar to the latter as its BNPP was 3.0-fold higher when grown with itself than under interspecific competition. *O. ficus-indica* doubled its BNPP under the dry as compared to the wet water regime when growing with itself but produced less BNPP and showed no water effect when grown under interspecific competition. *S. marginatum* showed no significant effect in its BNPP on the water treatment (Fig. 1d).

Competition index

Ricinus communis and *O. ficus-indica* showed aboveground competition in their direct interaction, with the lnRR for ANPP being 3.4-fold higher for *O. ficus-indica* than for *R. communis* (1.51 ± 0.31 mean ± SD versus 0.45 ± 0.23, respectively; Fig. 2a). This pattern of aboveground competition was unaffected by the water regime.
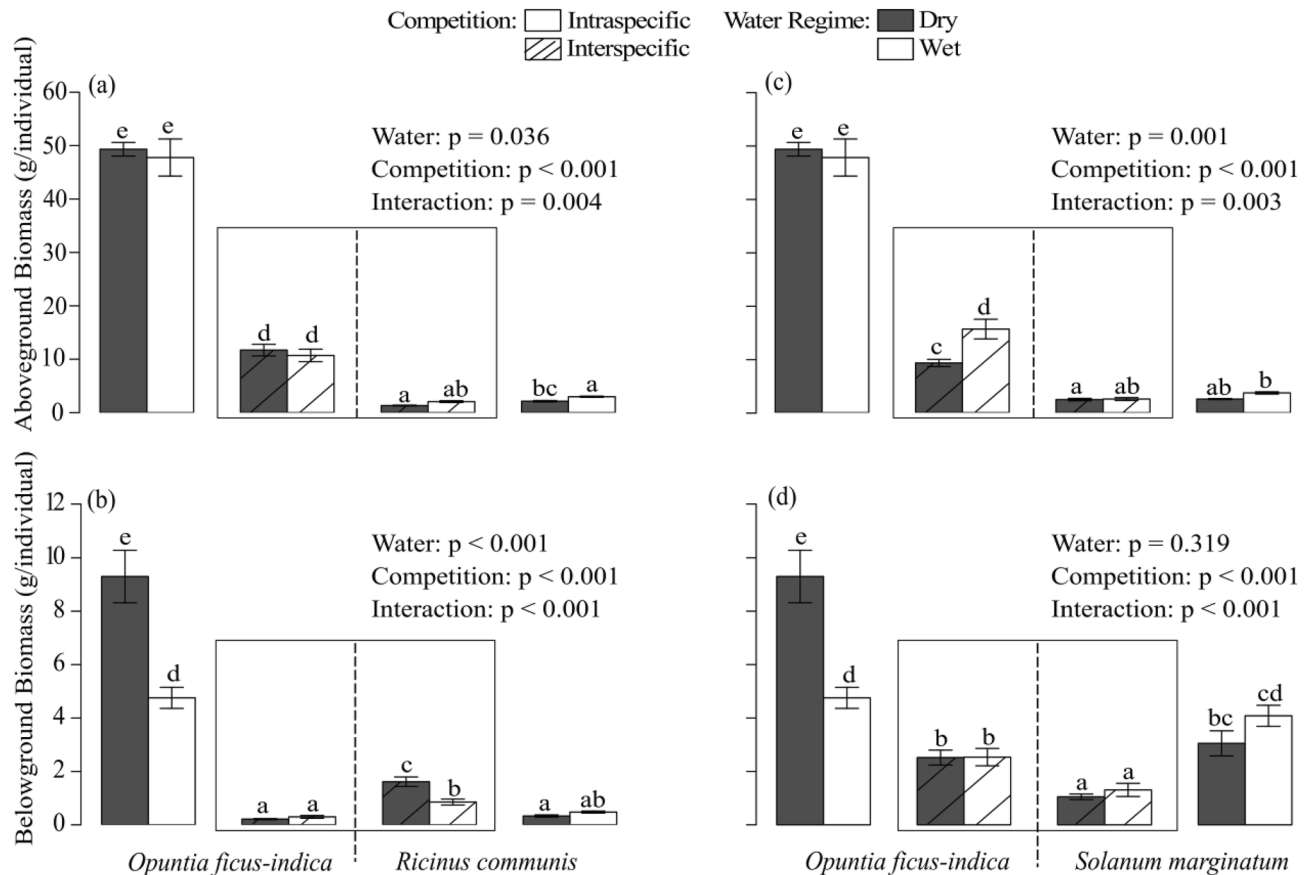
Figure 1. Aboveground (**a**, **b**) and belowground (**c**, **d**) biomass production (mean ± SD) of *Opuntia ficus-indica* and *Ricinus communis* growing in intraspecific competition or interspecific competition (**a**, **c**) and *Opuntia ficus-indica* and *Solanum marginatum* growing in intraspecific competition or interspecific competition (**b**, **d**) under wet (white) and dry (dark grey) conditions. Competition is a factorial variable with four levels: native-native, native-invasive, invasive-native, and invasive-invasive, with the biomass value of the first named in each pair in interspecific competition and the average biomass of both individuals per pot in case of intra-specific competition. Lowercase letters above the columns indicate homogeneous groups according to Tukey's post hoc test. The interspecific competition is indicated by diagonal hatching and solid boxes around the bars of those plants that grew together.

Belowground, the native *R. communis* was facilitated (− 1.00 ± 0.69, Fig. 2b) by *O. ficus-indica* which itself suffered strongly from high competition by the native species (3.35 ± 0.65; Fig. 2b). This pattern was significantly stronger for both species under dry than under wet conditions.

Solanum marginatum and *O. ficus-indica* showed aboveground competition in their direct interaction, which was 5.9-fold higher for *O. ficus-indica* than for *S. marginatum* (1.45 ± 0.44 versus 0.24 ± 0.33, respectively; Fig. 2c). This aboveground competition was 5.7-fold stronger for *S. marginatum* under wet as compared to dry conditions and 1.4-fold weaker for *O. ficus-indica* under wet as compared to dry conditions. Belowground, *S. marginatum* and *O. ficus-indica* showed about equal competition in their direct interaction (1.20 ± 0.46 versus 1.04 ± 0.52; Fig. 2d). For *S. marginatum*, belowground competition was unaffected by the water regime while competition increased 1.9-fold under dry as compared to wet conditions for *O. ficus-indica*.

Discussion

Opuntia ficus-indica, a highly successful invader of semiarid and arid ecosystems on all continents containing such conditions[28], was an inferior competitor to *Ricinus communis* and *Solanum marginatum*, two species native to the highlands of Eritrea where *O. ficus-indica* is also spreading vigorously. These findings stem from our greenhouse pairwise competition experiment offering valuable insights to a possible explanation of potential outcomes in a field setting. *O. ficus-indica* dropped in ANPP and BNPP about fourfold and 3 to 27-fold, respectively, when growing together with *R. communis* and *S. marginatum*. Competition indices indicated high competition for *O. ficus-indica* irrespective of the competing native, while the natives experienced less competition or even facilitation by *O. ficus-indica*. These findings reject the hypothesis that the successful invader is a superior competitor to the native species[73,74]. The majority of pairwise competition trials between invasive and native species supported that hypothesis[7]. The notable exceptions in that meta-analysis stem mainly from temperate grasslands, which are known to harbour native species with high competitive abilities that can resist invasions[75]. Based on this and the
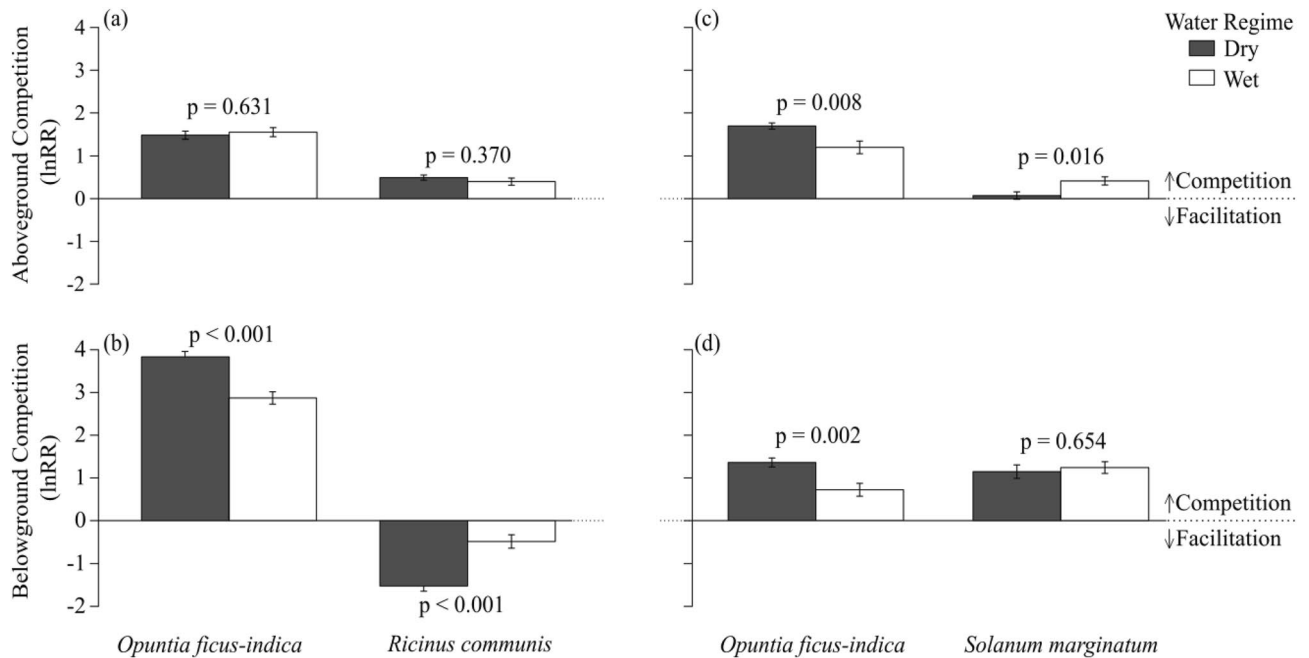
Figure 2. Relative competition intensity, according to the Logarithmic Response Ratio (lnRR) (mean ± SD), of the above (**a**, **b**) and belowground (**a**, **d**) biomass production for the pairwise competition experiment between the invasive *O. ficus-indica* and the native *Ricinus communis* (**a**, **c**) or the native *Solanum marginatum* (**b**, **d**). Negative values indicate a facilitative effect on the named species and positive values indicate competition for the named species. One-way ANOVA pairwise comparisons between the wet (white) and dry (dark grey) water treatments are provided.

competitive abilities found in our study, our invasive species should face strong resistance and have little success in invading native communities containing the two competitively superior native focal species. Surprisingly, that is not the case. *O. ficus-indica* spreads vigorously into areas containing those two native species[5]. So, the question arises: how can an inferior competitor be a successful invader?

The invasive *O. ficus-indica* produced several times more biomass than the natives, even under competition with the natives where it is doing much worse than on its own. Therefore, it 'outproduces' the competitively stronger natives in all cases except for BNPP with *R. communis*. Although we didn't quantify belowground biomass at transplantation to keep root systems intact, visual assessment revealed no significant differences among the three plant species. Thus, to better understand the role of competition in plant invasion, the relative biomass production of an invasive species compared to the native species should therefore be taken into consideration. Based on a meta-analysis of interspecific and intraspecific competition trials, Vilà and Weiner[7] found that mixtures of native and invasive species are less productive than native monocultures but not less productive than monocultures of the invasive plants. In our study, the interspecific mixtures produced, on average, 13.9 g aboveground biomass per pot, which is more than twice the production of the native species in monoculture (5.7 g) but nearly seven times less than the invasive species in monoculture (97.1 g). The numbers for BNPP followed a similar pattern, being 2.9 g for the mixture, 3.3 g for the native monocultures, and 14.1 g for the invasive monocultures, respectively. Comparing these numbers to the meta-analysis implies that our finding of a highly productive but weakly competitive invasive species might be an interesting exception rather than the rule.

The results of our experiment showed that competition by the native species generally increased for *O. ficus-indica* under the dry as compared to the wet treatment (Fig. 2). At first sight, this finding contradicts our second hypothesis which expected higher competitive power of *O. ficus-indica* under dry conditions. However, this weak competition should not be interpreted as a sign of reduced invasion pressure on the community. *O. ficus-indica* is a plant that has adapted to endure extreme environmental conditions and flourish in arid environments. By utilizing Crassulacean Acid Metabolism (CAM) photosynthesis, *O. ficus-indica* strategically minimizes moisture loss and enhances water-use efficiency, making it a highly drought-tolerant species that can cause pressure on the native community[76]. Moreover, the unique ability of *O. ficus-indica*'s fallen cladodes to undergo vegetative growth is a fundamental trait that contributes to its spread. This growth strategy enables *O. ficus-indica* to outgrow native species and establish a significant presence.

We based the water regimes of our experiment on pretrials that tested the water tolerance limits of the target species and found increased mortality of the native species right below our dry water regime. The ability of *O. ficus-indica* to survive well below this limit probably contributes greatly to its invasion success in dry ecosystems. Moreover, within the dry ecosystems, water availability becomes a major source of competition, favouring plants like *O. ficus-indica* which are capable of enduring the water shortages[19], but readily taking up large amounts of water as soon as it becomes available with its rapidly forming rain roots and storage in its succulent tissue[77]. Our pretrial showed that it even survived nine months without any water addition in our experimental setup

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(see Supplementary 1 online). This extreme drought tolerance is an important advantage for *O. ficus-indica,* as drought is frequent in the highlands of Eritrea[78]. The native species are expected to be adapted to what was the norm frequency and magnitude of drought, but climate change will result in stronger and more frequent drought events[39], which will challenge their survival. Disturbance in the native vegetation due to drought might therefore create gaps with little to no interspecific competition in which the invasive species can spread even more rapidly[17]. Notably, *O. ficus-indica* was also able to survive very wet periods according to our pretrials. Even complete submergence of the pots for three months did not kill the plants but resulted in roots growing on the surface of the water, probably seeking oxygen access (see Supplementary 1 online). Besides 'outproducing' native species by high biomass production, these extreme tolerance limits are another potential explanation for the global invasion success of *O. ficus-indica*.

The two native species showed interesting differences in their response to competition by *O. ficus-indica*. *R. communis* increased its BNPP under interspecific competition with *O. ficus-indica* when stressed with water shortage (dry water regime). This is reflected in the competition index indicating facilitation for *R. communis* by *O. ficus-indica* (Fig. 2). Fighting against *O. ficus-indica* belowground, however, did not help its general case as it was still 'outproduced' by *O. ficus-indica* aboveground. The ANPP of *O. ficus-indica* in interspecific competition with *R. communis* is quite remarkable when taking the very low BNPP due to high interspecific competition into consideration. *S. marginatum*, on the other hand, appeared to give in to the interspecific competition by *O. ficus-indica* belowground, as it showed decreased BNPP compared to the intraspecific interaction. *O. ficus-indica* is able to produce about 10 times as much root biomass in the presence of *S. marginatum* than in the presence of *R. communis*. Still, *S. marginatum* was successful in competing with *O. ficus-indica* aboveground, where it showed low competition, especially under dry conditions. Despite the efforts to compete with *O. ficus-indica* aboveground, it did not alter the overall outcome, as it was still 'outproduced' by *O. ficus-indica* aboveground. Potential explanations for the different behaviour of the native species in response to competition by *O. ficus-indica* might be that *S. marginatum* unlike *R. communis* is rather a drought-tolerant species that can better survive longer periods without water[62]. In any case, neither strategy appeared to be successful as both natives are clearly outperformed by *O. ficus-indica* in ANPP, irrespective of the water regime and despite them being superior competitors to *O. ficus-indica*.

Conclusion

A species successfully invading semiarid to arid ecosystems across the globe, *O. ficus-indica*, is an inferior competitor to two common and widespread native species of the highlands of Eritrea. One of the natives, *R. communis*, successfully competed with *O. ficus-indica* belowground, and the other native, *S. marginatum*, showed superior competition mainly aboveground. This finding contradicts the common implicit interpretation that successful invasive species have overall advantageous traits that make them stronger competitors than native species. Being vastly more productive, even under interspecific competition, and considerably more tolerant against water stress than the native species appears more important than competitive power, at least for invasions in semiarid to arid, open vegetation. Stronger and more frequent disturbance of the native vegetation by drought due to climate change will further accelerate the success of *O. ficus-indica*, as it is extremely drought tolerant and produces considerably more biomass in the absence of interspecific competition.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author upon reasonable request.

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Author contributions

Y.T. and J.K. contributed to the study conception and design. Material preparation, data collection and analysis were performed by Y.T. The pretrial experiment, design, data collection and analysis were performed by A.B. The first draft of the manuscript was written by Y.T. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Chapter III: Increased Plasticity in Invasive Populations of a Globally Invasive Cactus

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Increased Plasticity in Invasive Populations of a Globally Invasive Cactus

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Abstract: Biological invasions pose global threats to biodiversity and ecosystem functions. Invasive species often display a high degree of phenotypic plasticity, enabling them to adapt to new environments. This study examines plasticity to water stress in native and invasive *Opuntia ficus-indica* populations, a prevalent invader in arid and semi-arid ecosystems. Through controlled greenhouse experiments, we evaluated three native and nine invasive populations. While all plants survived the dry treatment, natives exhibited lower plasticity to high water availability with only a 36% aboveground biomass increase compared to the invasives with a greater increase of 94%. In terms of belowground biomass, there was no significant response to increased water availability for native populations, but plants from the invasive populations showed a 75% increase from the dry to the wet treatment. Enhanced phenotypic plasticity observed in invasive populations of *O. ficus-indica* is likely a significant driver of their success and invasiveness across different regions, particularly with a clear environmental preference towards less arid conditions. Climate change is expected to amplify the invasion success due to the expansion of arid areas and desertification. *Opuntia ficus-indica* adapts to diverse environments, survives dry spells, and grows rapidly in times of high-water supply, making it a candidate for increased invasion potential with climate change.

Keywords: phenotypic plasticity; biological invasions; *Opuntia ficus-indica*; non-native populations; greenhouse experiment

1. Introduction

Invasive species successfully establish and spread outside their native range to the detriment of the environment [1]. These biological invasions pose a significant threat to biodiversity and the functioning of ecosystems globally [2,3]. Non-native species are found in biogeographic regions outside their native range, overcoming unfamiliar environmental conditions and selective forces [4]. The rapid adaptation observed in some non-native species upon establishment in new environments has been suggested to explain their successful proliferation and invasive nature [5,6]. Several factors, such as competition for resources, allelopathy, enemy release, climate change, genetic variation and adaptation, contribute to the success of invasive species [7–9]. Moreover, a higher degree of phenotypic plasticity is one of the causes that drives an increase in the frequency and extent of plant invasions [10–12].

Phenotypic plasticity refers to an organism's capacity to modify its phenotype in response to environmental changes, enabling it to adapt its observable traits accordingly [13,14]. This adaptive ability of phenotypic plasticity is particularly significant in the context of plant invasions, as it empowers invasive species to acclimatize to novel

environments, enhancing their survival and reproductive success. Invasive plants tend to exhibit high levels of plasticity, allowing them to adjust their morphological, physiological, and reproductive traits in different environments [10,15,16].

In addition to the inherently high levels of plasticity observed at the species level, invasive populations can exhibit variations in plasticity when compared to native populations of the same species. Populations of invasive plants in introduced ranges are reported to show greater plasticity than populations in the native range [15,17]. Richards et al. [15] suggest that it is this greater phenotypic plasticity, among other causes, that contributes to the success of invasion by introduced plant species. Accordingly, Kaufman and Smouse [18] report that invasive populations in the introduced ranges of *Melaleuca quinquenervia*, a wetland tree species indigenous to eastern Australia, exhibit higher levels of plasticity in response to different water levels. Similarly, Sexton et al. [17] found significant genetic variation among different ecotypes of *Tamarix ramosissima* populations across its introduced ranges in North America. On the other hand, a common garden drought experiment between the plant populations of *Tanacetum vulgare* from its native range in temperate Europe and the invasive range in North America showed no significant interaction between range and treatment and as a result did not support the evolution of increased phenotypic plasticity in invasive populations [19]. Some invasive species have also been found to create increased intrapopulation genetic diversity once they have established outside of their native ranges [20], thus increasing their survival and adaptability.

Climate change will lead to warmer and drier conditions for large parts of the globe. Consequently, semi-arid and arid tropical regions might expand considerably [21], thereby increasing water stress for the native vegetation. As a cactus, *Opuntia ficus-indica* has the innate ability to survive in dry environments [22,23] and thrive in large areas that become warmer and drier [24]. *Opuntia ficus-indica*, native to Mexico, is a very drought-resistant cactus that is already invasive in arid and semi-arid environments in many parts of the world [25–29]. Recent genetic studies in Mexico have found a very high genetic diversity in this species and highlight the poor understanding of its population structure [30]. High levels of genetic diversity are also described for its invasive populations in Algeria [31], showing that some morphological characteristics were influenced by environmental factors. These morphological responses could potentially become important for understanding the underlying gene-by-environment relationships, referring to the interaction between an individual's genetic makeup and its environment, which can influence the expression of phenotypes [32]. *O. ficus-indica* is further described as an aggressive invader due to high drought and light tolerance [33]. Likewise, a drought experiment in Italy demonstrated high stress tolerance of locally naturalized *O. ficus-indica* populations, concluding that it will become an important threat to biodiversity conservation in the Mediterranean Basin in the near future [34]. Knowledge of the factors contributing to the invasiveness of *O. ficus-indica* will therefore be important in controlling its spread as the global climate shifts in its favor.

Here, we quantified phenotypic plasticity to water stress in populations from the native (Mexico) and invasive (Africa, Europe) ranges of *O. ficus-indica* in a greenhouse experiment. We hypothesized that phenotypic plasticity in response to water availability is beneficial for invasion success in (semi-)arid environments. Therefore, we anticipated that populations from the invasive ranges would exhibit greater plasticity, displaying improved survival under drought conditions and a more significant increase in biomass production when exposed to higher water availability compared to populations from the native range.

2. Results

Opuntia ficus-indica plants from the invasive range showed more plasticity to water availability than plants from the native range in aboveground net primary production (hereafter ANPP) (ANOVA interaction range x water treatment: F = 8.73, p = 0.004; Figure 1a). Quantitatively, plants from the native range increased their ANPP from the dry

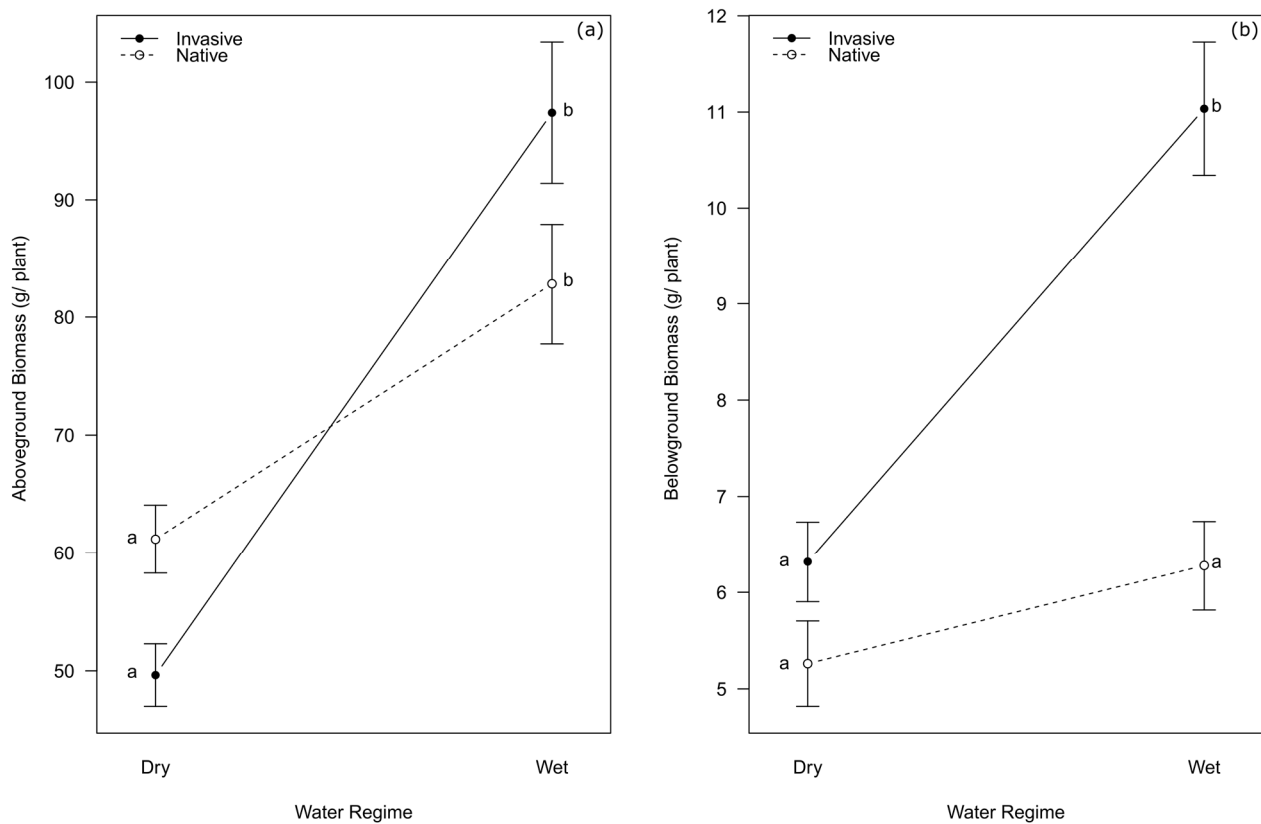to the wet treatment by only 36%, while the plants from the invasive range increased ANPP by 96%.

Figure 1. Aboveground (**a**) and belowground (**b**) biomass production (mean $\pm$ SE over all populations) of *Opuntia ficus-indica* from the native range (dashed line) and invasive range (solid line) growing under wet and dry regimes. Lowercase letters adjacent to the error bars indicate homogeneous subgroups according to Tukey's post hoc test. See Appendix A (Figure A1) for the response of individual populations. As a measure of plasticity, ANPP increased 1.4-fold and 2-fold from dry to wet for the native and the invasive populations, respectively; BNPP increased 1.2-fold and 1.8-fold.

The belowground net primary production (hereafter BNPP) of *O. ficus-indica* plants from the native range showed no significant increase between the dry and wet treatments (p = 0.501). In contrast, the BNPP of plants from the invasive range exhibited a strong increase of 75% (p < 0.001; ANOVA interaction range x water regime: F = 10.32, p = 0.002). Moreover, no significant difference was observed between the native and invasive ranges in terms of belowground biomass in the dry treatment (p = 0.783), but a significant difference (p = 0.034) was observed in the wet treatment, with the invasive range displaying a 76% higher belowground biomass production than the native range under wet conditions (Figure 1b).

All individuals survived the dry treatment. Populations from more humid origins, however, showed stronger responses to additional water than populations from more arid origins for the aboveground biomass (p = 0.018; Figure 2a), but there were no significant differences observed in the belowground biomass production (p = 0.143; Figure 2b).
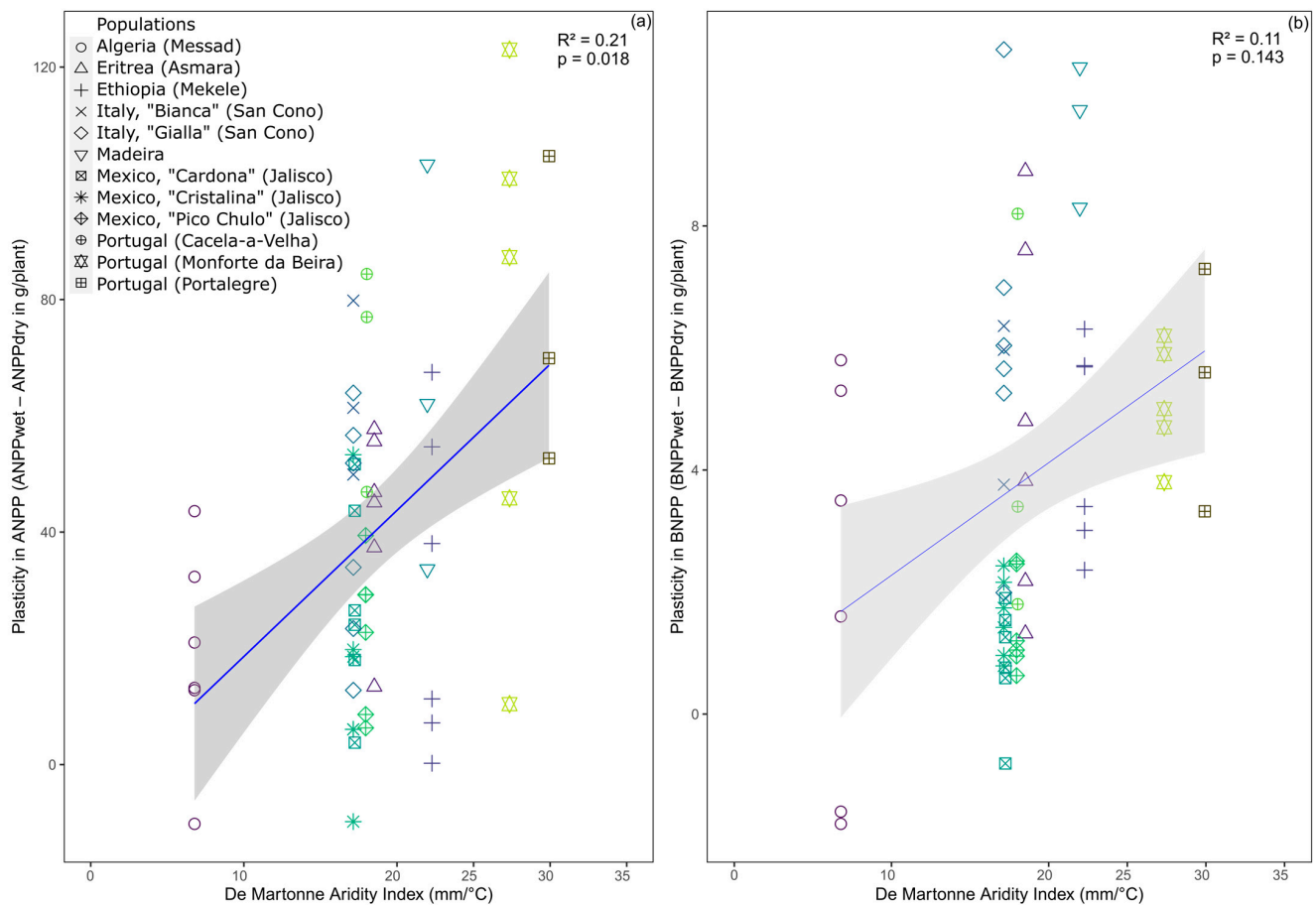
Figure 2. Opportunism to water availability increases with mean annual water availability at the origin of the populations of *Opuntia ficus-indica*. Depicted is the De Martonne aridity index at the populations' origins (values from 0 to 10 indicate arid climates, 10–20 semi-arid, 20–24 Mediterranean, 24–28 semi-humid, 28–35 humid) and the opportunism as the difference between the aboveground (**a**) or belowground (**b**) net biomass production in the wet versus the dry treatment, i.e., the degree of plasticity in biomass production. The plasticity in net biomass production was calculated by randomly assigning pairs of wet and dry treatments for each population. Symbols show original data points. Linear mixed-effects models with population as a random effect and their 95% CIs are displayed.

3. Discussion

The results of our experiment provide evidence for higher levels of plasticity in the response of biomass production to water availability in invasive populations of *Opuntia ficus-indica* compared to native populations. Our findings support previous reports of higher levels of plasticity in plants from invasive populations compared to their native counterparts [10,15–17]. The success of invasive species can generally be attributed to two factors regarding the response of fitness traits to environmental variation: (1) their ability to maintain fitness across diverse environments; and (2) their capacity to enhance fitness in favorable environments [35–37]. According to our results, *O. ficus-indica* fulfills the second factor more strongly in its invasive than in its native populations. An important point to emphasize is that in addition to the invasive populations of *O. ficus-indica* exhibiting improved water utilization in the wet treatment compared to native populations, all individuals survived the dry treatment. While taking advantage of favorable conditions is beneficial, the capacity to withstand unfavorable conditions, the second factor, is equally important for long-term survival and success. The ability of an organism to increase its own fitness in a changing environment is a competitive advantage over species that lack this ability [38,39]. Plants in general can and have adapted in instances of rapid climate change to maximize their fitness in such variable environments [40]. Invasive plants have proven

their capacity to adapt to new environmental conditions and can therefore be expected to also adapt better to changing environmental conditions caused by climate change than presumably less plastic, native species, thus enhancing their advantage [41].

The invasive populations in our study exhibited a greater increase in aboveground biomass under favorable conditions than the native populations. This, coupled with the positive correlation between the environmental conditions at the origin of the populations and the observed increased plasticity (Figure 1a), strongly suggests that plasticity itself is an adaptive trait in *O. ficus-indica*. These results further imply that the species has undergone a rapid adaptive response in plasticity to higher water availability, as the species reached some of its invasive ranges only a few generations ago [28]. The phenotypic changes observed in *O. ficus-indica* within its introduced ranges are indicative of its adaptivity in response to novel environmental conditions [42], and this adaptive potential can be associated with the successful tolerance and invasion of broad geographic areas. While plasticity is certainly not always adaptive, it sometimes is and appears to help *O. ficus-indica* cope with diverse and fluctuating environmental conditions [17,43]. The potential to increase belowground biomass production in response to high water availability appears to be an important and adaptive difference between the invasive and native populations of *O. ficus-indica* (Figure 1b). Cacti are generally recognized for their ability to rapidly develop new roots, enabling efficient water uptake as soon as soil water becomes available [44–46]. These rapidly growing roots then disappear again when the soil dries up [47]. We speculate that, in addition to being drought-tolerant [48,49], this ability to dynamically adjust the rooting system has fostered the adaptation of invasive populations to Mediterranean and even sub-humid conditions.

Increased plasticity of *Opuntia ficus-indica* in its invasive populations makes its invasion success even more threatening, as it does not appear to lose its ability to withstand dry periods while making better use of wet conditions. This is supported by the fact that the biomass production of the invasive populations was not significantly lower than that of the native populations in the dry treatment (Figure 1). The ability of *O. ficus-indica* to endure dry periods and exhibit rapid and vigorous growth in response to increasing water availability [33] will significantly contribute to its success in invading new habitats in warming, drying and more fluctuating climate conditions of the future [21]. Here, we have no comparison to growth rates of native species under the same conditions, but we hypothesize that *O. ficus-indica* can tolerate drought better than almost any other species [27,50,51]. Additionally, considering the strong growth observed over the 26-month duration of this experiment, it is likely to effectively compete with native species during wet periods, making it an almost perfect invader in environments characterized by highly fluctuating water availabilities including long and extreme dry periods.

In conclusion, the results of this study demonstrate that *O. ficus-indica* exhibits higher levels of phenotypic plasticity in response to water availability in invasive populations than in native ones. Populations showing a positive relationship between plasticity and water availability at their origin further indicate a quick and beneficial adaptation of plasticity. Conserved water stress tolerance coupled with increased growth under wet conditions in invasive compared to native populations suggest that *O. ficus-indica* will further benefit from climate change, particularly from increased fluctuations in water availability, and continue or even accelerate its spread into native plant communities throughout arid, semi-arid, Mediterranean, and even subhumid ecosystems.

4. Materials and Methods

4.1. Study Species

Opuntia ficus-indica (L.) Mill. is an evergreen perennial cactus that can grow up to 5 m in height. The species has succulent stems that are formed as a sequence of flattened segments called cladodes, which generally have an elliptical base that supports the greatly enlarged and flattened upper portion. *Opuntia ficus-indica* has spines, morphologically corresponding to leaves. Its flowers (5–10 cm in diameter) are sessile and solitary, and the

fruits are berries that are 4–8 cm in diameter [52] with an average of 273 seeds per fruit [53]. Nieddu and Chessa [54] found the germination of the *O. ficus-indica* seeds reaching up to 90% in growth chambers with a day/night temperature of 30/20 °C, but only reaching 55% when seeds were kept at room temperature and 43% when seeds were placed outdoors. The seeds are usually dispersed after consumption by humans, birds, and other animals (endozoochoric). Furthermore, vegetative propagation occurs through cladodes readily taking root upon falling to the ground and conspicuous patch formation is an important factor in the persistence of local populations of the plant, although seedling recruitment is essential for expanding the geographic range and establishment in new areas [52].

4.2. Experimental Design

The greenhouse drought experiment was carried out from September 2020 to November 2022 at Greifswald, Germany. We planted the seeds of *O. ficus-indica* from a total of 12 populations (Table 1): three from its native range in Mexico (Jalisco region), three from Africa (Algeria, Eritrea, Ethiopia), one from the island of Madeira off the coast of Africa, and five from Europe (Italy and Portugal), as shown in Figure 3. In Mexico and Italy, different cultivars were collected in order to capture a broad spectrum of genotypes. Taxonomically, the status of the Mexican genotypes "Pico chulo," "Cristalina," and "Cardona" is still debated, and some authors see our third genotype as a different species [55,56]. Here, we treat all of them as populations of *O. ficus-indica*, thereby potentially erring towards higher genetic diversity and presumably also phenotypic plasticity in the native range. Consequently, any evidence supporting our hypothesis of higher plasticity in the invasive populations is conclusive, while no difference between the native and non-native populations would be inconclusive.

Table 1. Populations of *Opuntia ficus-indica* used in this study. De Martonne aridity values from 0 to 10 indicate arid, 10–20 semi-arid, 20–24 Mediterranean, 24–28 semi-humid, and 28–35 humid climate conditions [57].

Range	Area of Origin	Approximate Collection Coordinates	De Martonne Aridity Index (mm/°C)
Non-native	Algeria (Messaad)	34.15212° N, 3.516667° E	7
Non-native	Eritrea (Asmara)	15.23135° N, 38.89911° E	19
Non-native	Ethiopia (Mekele)	14.24886° N, 39.43692° E	22
Non-native	Madeira	32.64838° N, 16.96288° W	22
Non-native	Italy, "Gialla" (San Cono)	37.29390° N, 14.37002° E	17
Non-native	Italy, "Bianca" (San Cono)	37.29390° N, 14.37002° E	17
Non-native	Portugal (Portalegre)	39.27290° N, 7.436978° W	30
Non-native	Portugal (Monforte da Beira)	39.75232° N, 7.281897° W	28
Non-native	Portugal (Cacela-a-Velha)	37.15625° N, 7.546661° W	18
Native	Mexico, "Pico Chulo" (Jalisco)	21.68530° N, 101.4950° W	18
Native	Mexico, "Cristalina" (Jalisco)	22.20615° N, 101.5752° W	17
Native	Mexico, "Cardona" (Jalisco)	21.80851° N, 101.3619° W	17

The cacti were grown in a climate-controlled greenhouse at an average 40% humidity and with a temperature range of 12 °C (for 12 h at night) and 20 °C (for 12 h a day), and windows were set to allow air flow if temperature reached 16 °C (night) or 22 °C (day) for natural cooling. Supplemental lighting, allowing for an additional 115 μmol/m²s of photosynthetically active radiation (PAR) to the ambient conditions at pot level, was also provided for 12 h per day from 6:00 to 18:00 using SON-KE 400 high-pressure discharge lamps (DH Licht GmbH, Wülfrath, Germany). The positions of the pots within the greenhouse were frequently interchanged to ensure similar environmental conditions and reduce edge effects or the like.
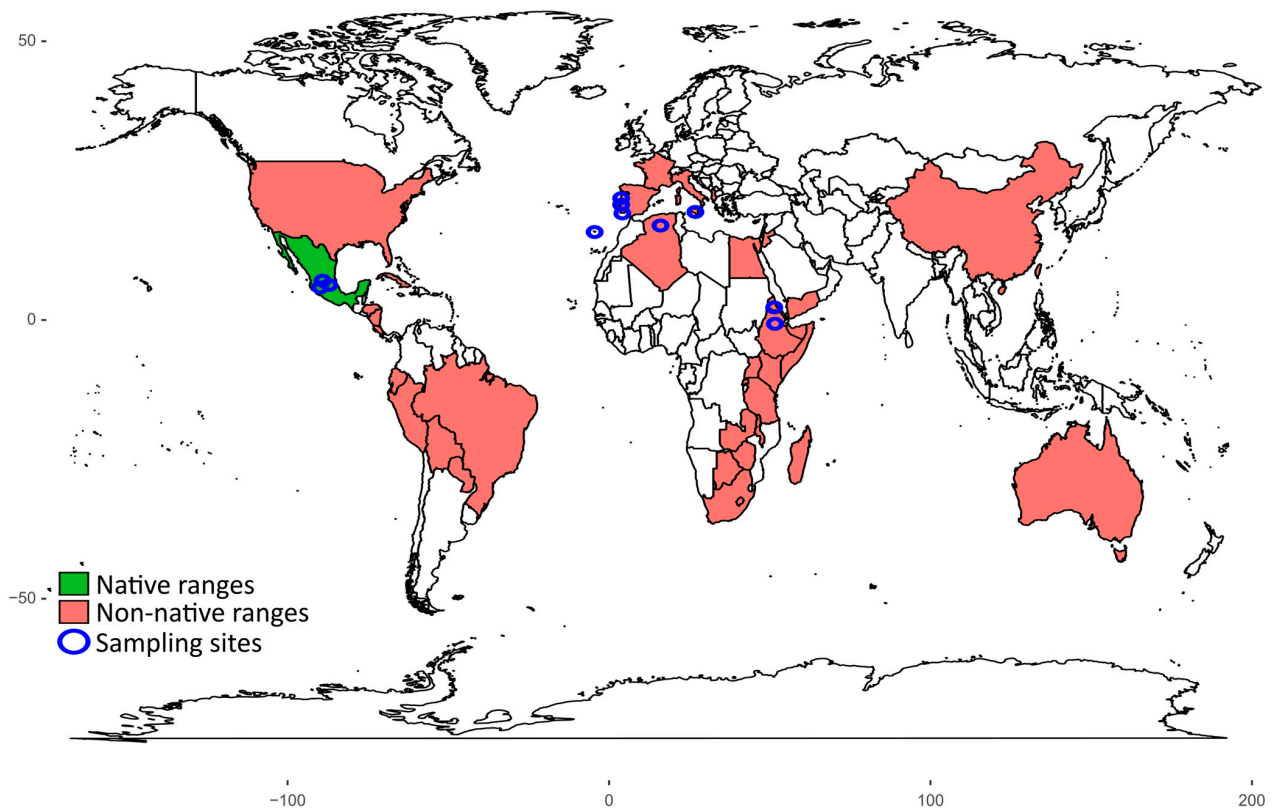
Figure 3. The distribution of *Opuntia ficus-indica*, based upon presence in countries with native range in green (Mexico) and non-native range in light red as reported by Bakewell-Stone [28]. The blue circles indicate the locations where the populations used in this study were collected.

Plasticity was quantified based on two levels of water availability, depicting dry and wet environments. We measured plasticity by examining how the plant's phenotype, i.e., above- and belowground biomass, responded to these two environments, comparing the differences in *O. ficus-indica*'s traits between the dry and wet conditions.

The substrate was a mixture of 75% forest soil (loamy sand) and 25% quartz sand. All plants were raised from seeds that were sown in January 2019. After being transplanted into their respective two-liter target pots on 18 September 2020, all plants exhibited similar heights of approximately 40 cm. From a total of 120 pots, the plants from each population (n = 10) were randomly assigned to the two water availability treatments (n = 5), namely, a "wet" treatment that received 160 mL of water twice per week, and a "dry" treatment that received 40 mL of water twice per week. The watering regimes were based on a preliminary pot experiment, exposing 16 plants from Eritrea to a gradient of water availability ranging from no water up to 260 mL twice a week over a period of nine months. The experiment was conducted in the same greenhouse and using the same experimental settings, including pot size, substrate, plant material, and environmental conditions, as the main experiment. All plants survived the pretrial, even though the growth of the plants exposed to drought on the lower end of the gradient, mainly at and below 40 mL, was impeded. The plant exposed to 40 mL, our dry treatment here, showed 80% less aboveground biomass than the wet treatment (160 mL). In a subsequent recovery experiment, the plants that were previously subjected to drought showed rapid aboveground biomass recovery within a span of five days. Additionally, the plant that received the highest amount of water was submerged in a bucket of water for three months and displayed no signs of stress. More details of the pretrial experiment can be found in Appendix B, Figures A2 and A3.

4.3. Response Parameters

We quantified ANPP and BNPP at the end of the experiment. We carefully removed each plant from its pot and cut all roots from the stems. The belowground biomass was then gently washed free from the substrate by rinsing it into a coarse sieve so that the substrate was washed away and the roots and rootlets remained. Above and below-ground biomass was dried in separate paper bags for five days at 60 °C and 100% ventilation and the dried samples were subsequently weighed to one decimal point of a gram.

4.4. Statistical Analyses

The response variables (ANPP and BNPP) were analyzed by fitting a linear mixed-effects models (lmerTest package, version 3.1-0; [58]), with the explanatory factors being water regime (wet/dry) and range of the species (native/invasive), including their interaction and population identity as a random effect. ANOVA was then applied to extract the significance of the explanatory factors of the mixed model. Single models were run for each response parameter (ANPP and BNPP) for a total of two ANOVA analyses. Tukey's HSD post hoc tests [59] were used to assess the significance of differences in pairwise comparisons for significant interaction terms.

Moreover, we calculated the De Martonne aridity index [57] as an explanatory factor to identify climatic aridity at the origins of all populations based on temperature and precipitation data for the period 1970–2000 [60]. The De Martonne index is expressed as:

$$I_{DM} = \frac{P}{T_a + 10}$$

where P is the annual amount of rainfall (in millimeters) and T_a is the mean annual air temperature (in degrees Celsius). We tested for a potential relationship between aridity at the origin of the populations and plasticity in growth under different water availability by linear mixed-effects model regression between the De Martonne aridity index as an explanatory variable and the difference between growth in the wet and dry treatments as a response variable. Pairs of wet and dry samples were assigned randomly within each population, and population identity was included as a random effect in the model.

Parametric assumptions were checked for all ANOVA and regression models by examining the diagnostic plots (residuals versus fitted plots for homoscedasticity of the residuals and normal qq-plots for normal distribution of residuals) [61]. When necessary, the ANPP and BNPP datasets were log- or square root-transformed to meet the assumptions. The regressions with the aridity index did not require transformations. For graphical visualizations, the function lineplot.CI in the R package sciplot [62] and ggplot2 [63] were used. All statistical analyses were performed in R version 4.2 [64].

Appendix A

Figure A1. Opportunism to water availability for all populations of *Opuntia ficus-indica* used in the study. Aboveground biomass (**a**) and belowground biomass (**b**) under wet and dry regimes. The solid lines indicate the invasive populations, and the dashed lines indicate the native populations (Mexico) of *O. ficus-indica*. The plasticity in net biomass production was calculated by randomly assigning pairs of wet and dry treatments, respectively, for each population. Linear mixed-effects models with the population as a random effect and their 95% CIs are displayed.

Appendix B. Water Tolerance Limits of the Globally Invasive Cactus *Opuntia ficus-indica*

The tolerance limits of *Opuntia ficus-indica* regarding water supply were examined by monitoring growth (Figure A2a), biomass production (Figure A2b,d), water content (Figure A2c) and soil water potential (Figure A3). Sixteen plants from Eritrea were subjected to an irrigation gradient (0 to 260 mL of water per week) for nine months, four were then observed in a recovery experiment for another three months. After the drought and recovery experiment, the plants' biomass and water content were determined. All plants survived, even though the one subjected to complete drought throughout the trial did not grow. All other plants also showed growth, which was reduced up to a water addition of 60 mL per week and did not change further above that limit. The plants that were previously subjected to drought also showed rapid signs of recovery within five days of the start of the recovery experiment. Concerning drought tolerance, *O. ficus-indica* can survive droughts that last up to nine months and recover quickly. Surprisingly, no sign of reduced performance was found towards the wet end of the gradient. We conclude that *O. ficus-indica* has extremely broad tolerance limits regarding water supply, potentially allowing it to thrive in many regions of the world.
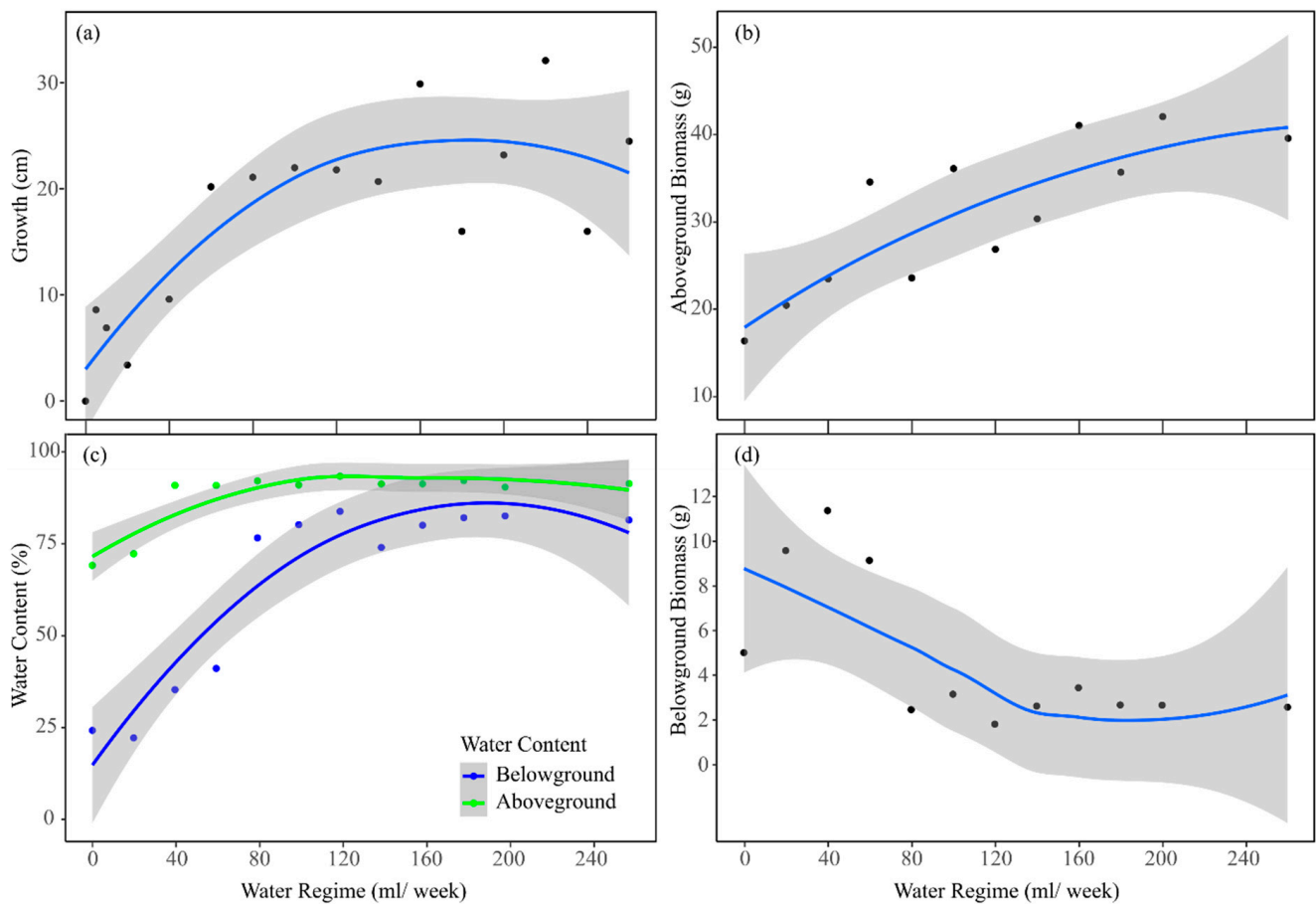
Figure A2. Growth (**a**), aboveground biomass (**b**), water content (**c**), and belowground biomass (**d**) at the end of the drought experiment. Dots are original data points, and lines show the smoothed local polynomial regression fitting (loess). 95% confidence intervals are displayed in grey. This pretrial aimed to observe potentially nonlinear patterns of response variables along the water availability gradient. A powerful tool to answer this kind of question is gradient experiments that maximize treatment levels by minimizing replication [65]. To unravel these response patterns, a graphical analysis was performed. Each response parameter was plotted over the water gradient and smoothed conditional means were calculated by local polynomial regression fitting using the "loess" function, implemented in R [64]. Span was adjusted to produce smooth curves without multiple local extrema based on the assumption that multiple maxima are unlikely in an autecological setting without competition. Confidence intervals (CIs) displayed around the conditional means were used to assess the significance of effects at a level of $\alpha = 0.05$. The environmental gradient was considered to have a significant effect if a straight horizontal line could not be fitted inside the 95% CI [66].
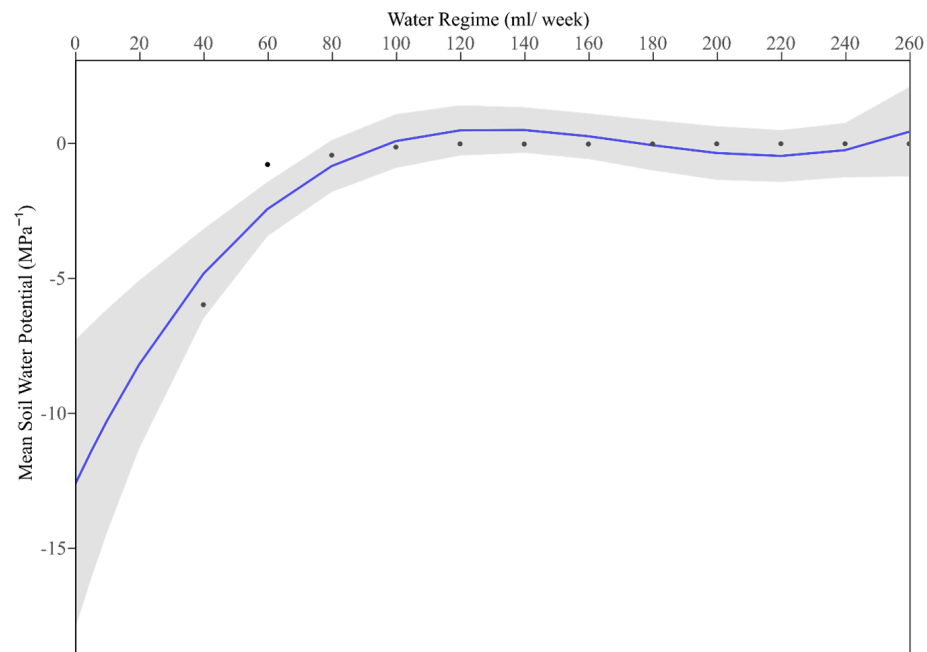
Figure A3. Mean water potential calculated from the entire period of the drought experiment. Dots are the mean data points, and lines show the smoothed local polynomial regression fitting (loess). 95% confidence intervals are displayed in gray. The sensors used to measure the soil water potential (SWP) had different minima and maxima. We were not aware of the limitations when the sensors were placed in the pots for the experiment. The values of the plants from both the extreme sides of the gradient were influenced by the sensors' lower limit or higher limit, which led to missing data for the driest treatments p0 to p20, where the SWP dropped below the lower limit of the sensors (Teros 21 generation 1:2 MPa^{-1}). As a result, these plants' SWPs are not included in this figure's SWP parameter, but we extrapolated the spline so that it reaches 0.

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Additional Documents

Eigenständigkeitserklärung

Hiermit erkläre ich, dass diese Arbeit bisher von mir weder an der Mathematisch-Naturwissenschaftlichen Fakultät der Universität Greifswald noch einer anderen wissenschaftlichen Einrichtung zum Zwecke der Promotion eingereicht wurde.

Ferner erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine anderen als die darin angegebenen Hilfsmittel und Hilfen benutzt und keine Textabschnitte eines Dritten ohne Kennzeichnung übernommen habe.

Yohannes B. Tesfay

Data availability

All primary data that was collected during the PhD studies is stored on the primary data server of the University of Greifswald. All manuscripts refer to supplementary material, which is attached to this thesis (USB disk). The USB disk also contains all individual manuscripts contributing to this thesis and the primary data as it is stored on the primary data server.

Curriculum vitae

YOHANNES B. TESFAY

EDUCATION

Since 10/ 2019	PhD Candidate
	University of Greifswald, Germany
	Institute of Botany and Landscape Ecology
09/2013 – 07/2015	MSc in Biology - Botany
	Eritrea Institute of Technology
	College of Science, Department of Biology, Asmara, Eritrea
09/2006 – 07/2011	BSc in Biology
	Eritrea Institute of Technology
	College of Science, Department of Biology, Asmara, Eritrea

GRANTS/ AWARDS

10/ 2019 – 01/ 2024	Doctoral Research Grant – DAAD
10/ 2019 – 01/ 2024	Associate PhD student - RESPONSE, University of Greifswald
04/ 2019 – 09/ 2019	Grant – German course – DAAD
03/ 2019	Award - Landesgraduiertenförderung, Universität Greifswald, Deutschland
11/2018 – 03/2019	Research scholarship - DAAD short-term scholarship

WORK EXPERIENCE

Since 01/ 2021	Progwise.net: Typescript React and GraphQL Fullstack Software Development: Lessons, self-learning, and practice
08/2015 – 11/2018	Lecturer, researcher, and supervisor
	Eritrea Institute of Technology
	College of Science, Department of Biology, Asmara, Eritrea.
08/2011 – 08/2013	High School Teacher: - Biology, Chemistry and English
	Nakfa Secondary School, Ministry of Education, Eritrea.

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List of publications and other scientific achievements

Tesfay, Y.B., Blaschke, A. & Kreyling, J. An inferior competitor is a successful invader due to its stress tolerance and productivity. *Sci Rep* 13, 20694 (2023). https://doi.org/10.1038/s41598-023-48152-y

Tesfay, Y.B., Blaschke, A., Ashley, N., Portillo, L., Scalisi, A., Adli, B., Kreyling, J. Increased Plasticity in Invasive Populations of a Globally Invasive Cactus. *Plants* 12, 3287 (2023). https://doi.org/10.3390/plants12183287

Tesfay, Y.B., Kreyling, J. The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea. *Biol Invasions* 23, 433-442 (2021). https://doi.org/10.1007/s10530-020-02373-8

Hubert, S., Borg-Dahl, M., **Tesfay, Y.B.**, Beil, I., Urich, T., Kreyling, J., Do Volcanoes Fertilize the Globe? Increased Plant Productivity and Restructured Soil Microbiome in a Controlled Experiment. SSRN Preprint (2023). http://dx.doi.org/10.2139/ssrn.4572289

Biniam, Y., **Tesfay, Y.B**., Kunduru, S.R. Ethnobotanical study of medicinal plants in sub region Logo Anseba, Region Gash Barka, Eritrea. IOSR *Journal of Pharmacy and Biological Sciences* (IOSR-JPBS), e-ISSN: 2278-3008, p-ISSN:2319-7676. Volume 11, Issue 4 Ver. IV, pp. 63-73 (2015). https://doi.org/10.9790/3008-1104046373

Tesfay, Y.B., Ecology and Ethnobotany of *Euphorbia abyssinica* in sub region Logo Anseba, Gash Barka Region, Eritrea. (2015). M.Sc. Thesis. Eritrea Institute of Technology, Eritrea.

NEOBIOTA INTERNATIONAL CONFERENCE ON BIOLOGICAL INVASIONS

12.09. – 16.09.2022, Tartu, Estonia

Yohannes B. Tesfay, Annika Blaschke and Jürgen Kreyling. An inferior competitor is a successful invader due to its stress tolerance and productivity. (**talk**)

GFÖ CONFERENCE: SCIENCE IN TRANSITION, SCIENCE FOR TRANSITION

31.08 – 03.09.2021, Braunschweig, Germany

Yohannes B. Tesfay and Jürgen Kreyling. The invasive *Opuntia ficus-indica* homogenizes native plant species compositions in the highlands of Eritrea. (**talk**)

Summer school - Dispersal and landscape approaches. University of Greifswald, Germany, 21/10 – 23/10/2020

Workshop - Project management in academia. University of Greifswald, Germany, 17/02/2020

Summer School on Genetic Adaptation and Molecular Genetic Approaches. Hiddensee, Germany, 07/10 – 10/10/2019

Workshop - Academic writing. University of Greifswald, Germany, 01/10 – 02/10/2019

Workshop - Good scientific practice. University of Greifswald, Germany, 07/02/2019

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