Introduced garden plants are strong competitors of native and alien residents under simulated climate change

Running head: Ornamental plant invasions and climate change

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Abstract

1) Most invasive plants have been originally introduced for horticultural purposes. Still, most alien garden plants have not naturalized yet, probably due in part to inadequate climatic conditions. Climate change may alter this, but few experimental studies have addressed this for non-naturalized alien garden plants, and those that have, addressed only singular aspects of climate change.

2) In a greenhouse experiment, we examined the performance of nine non-naturalized alien herbaceous garden plants of varying climatic origins in response to simulated climate warming and reduced water availability, in a factorial design, as projected for southern Germany. To assess their invasion potential, we grew the species in competition with resident native and already-naturalized alien species.

3) Reduced watering negatively affected non-naturalized garden plants, as well as the native and naturalized competitors, particularly at higher temperatures. However, non-naturalized aliens performed better relative to competitors when temperatures increased. Naturalized and native resident competitor responses to climate change were both negative, but across climate treatments, non-naturalized aliens, irrespective of their climatic origins, performed better against native than against naturalized competitors.

4) *Synthesis.* We conclude that relative performance compared to resident species may increase for non-naturalized alien garden plants under climate change, as resident species become less competitive. Ongoing climate change is therefore likely to promote naturalization of commonly-planted alien herbaceous species.

Introduction

Preventing introductions of new, potentially invasive species is a central objective in invasive species management, as their elimination is notoriously difficult, if not impossible, once they have become naturalized (Wittenburg & Cock, 2005). However, usually little attention is paid to the thousands of alien garden plant species which have already been introduced and have not yet established (i.e. become naturalized *sensu* Richardson *et al.*, 2000) outside cultivation (van Kleunen *et al.*, 2018), even if they have displayed naturalization potential in other regions of the globe (Essl *et al.*, 2011). In addition to being a primary pathway of introduction (Hulme, 2011), horticulture also often selects and breeds species with certain traits that are typically associated with invasion success (Anderson *et al.*, 2006; Kitajima *et al.*, 2006; Trusty *et al.*, 2008; Pemberton & Liu, 2009; Chrobock *et al.*, 2011; Moodley *et al.*, 2013; Maurel *et al.*, 2016). The garden flora thus constitutes a major source of potential invasive species, which have already been introduced.

The naturalization success of alien plant species is often influenced by climatic suitability (Feng *et al.*, 2016; Haeuser *et al.*, 2017; Mayer *et al.*, 2017). As many alien garden plants in temperate regions come from warmer, low-latitude regions (Van der Veken *et al.*, 2008), these species can survive and grow in garden environments but cannot establish self-sustaining populations in the wild yet. In other words, these alien garden plants are currently still outside their fundamental climatic niches but are inside their tolerance climatic niches (*sensu* Sax *et al.*, 2013). It has been suggested that some recent naturalization events have been triggered by climate change (Walther *et al.*, 2007; Bellemare & Deeg, 2015). With ongoing climate change, more garden species may experience increased climatic suitability, and are therefore more likely to escape cultivation and become naturalized, and possibly invasive. Indeed, Dullinger *et al.*

(2017) predicted, based on distribution modelling, that climate change will cause an overall increase in the naturalization risk of alien garden plants in Europe.

Species will undoubtedly respond differently to the various aspects of climate change (Williams *et al.*, 2007), and it is unclear how this variation in responses will affect future plant invasions. Studies experimentally assessing potential responses of invasion dynamics to climate change are not uncommon (e.g. Pattison & Mack, 2008; Manea *et al.*, 2016; Liu *et al.*, 2017), but their focus is typically limited to individual climatic components (e.g. Frei *et al.*, 2014; Schrama & Bardgett, 2016; Haeuser *et al.*, 2017). Other studies used reciprocal transplant experiments, which do not allow for the isolation of the effects of individual climatic components and other environmental factors that covary (e.g. Pattison & Mack, 2008). Moreover, it has been shown that invasion dynamics can be unpredictable when different aspects of climate change (e.g. altered precipitation and climate warming) act in concert (Bradley *et al.*, 2010), but in general such interactions have been little explored. Furthermore, most studies on effects of climate change on biological invasions focus on alien species that are already invasive, whereas experimental studies on responses of non-naturalized alien garden plant species are rare (but see Haeuser *et al.*, 2017).

Here, we tested experimentally how non-naturalized herbaceous alien garden species in southern Germany will respond to the combined effects of increased temperature and reduced water availability. Examining these factors in combination is important, because, in addition to potentially experiencing direct effects of increased temperatures, plants face reduced soil moisture levels and higher evapotranspiration. There is also strong potential for reduced precipitation in the form of extended drought periods, as predicted for southern Germany (LUBW, 2013). These may have compounding effects that warrant consideration. Furthermore, species will likely vary in their responses to climate change (Williams *et al.*, 2007), so it is important to use more than one species to test more generally how non-naturalized alien species respond, and to identify factors that explain variation in responses among species (van Kleunen *et al.*, 2014). In a previous study, we found that differences in colonization potential between non-naturalized alien garden plants of different climatic origins were reduced under increased temperatures (Haeuser *et al.*, 2017). Because garden species from different climatic origins may also respond differently to the compounding effects of reduced precipitation, we also assessed whether climatic origin plays a role in responses to a changing precipitation regime.

Because the future naturalization potential of alien species may be affected by changes in competition dynamics (Gilman *et al.*, 2010; Haeuser *et al.*, 2017), we grew the alien garden species in competition with resident grassland species, predominantly perennial herbs. While experiments on competition between aliens and residents typically limit the resident species pool to native species, naturalized alien species also represent a significant proportion of the current resident flora in many parts of the world (van Kleunen *et al.*, 2015; Pyšek *et al.*, 2017). This may matter for potential newcomers, because the naturalized and native resident species may respond differently to climate change. For example, it has been shown that naturalized species, compared to native species, are less negatively affected by warming (Haeuser *et al.*, 2017) and that invasive alien species frequently take advantage of warming (Liu *et al.* 2017). The status of the resident species may thus affect the strength of competition faced by newcomers, and the latter may be more likely to naturalize under climate change if they perform better than both native and naturalized residents. We therefore included both native and naturalized species as competitors in our experiment.

In this study, we address the following questions: 1) how will increased temperatures and reduced water availability affect the performance (absolute survival, growth and reproduction) of non-naturalized alien garden species (i.e. the target species), and will this vary between species with different native climatic origins? 2) How will the two climate change treatments affect the absolute performance of competing resident species, and will effects differ depending on whether the competing resident is native or naturalized? 3) How will the climate-change treatments affect the performance of target species relative to the performance of resident competitors, and will effects vary depending on the native climatic origin of the target species and the status (native, naturalized) of the competitor?

Materials and Methods

Study species and pre-cultivation

As target species, we selected nine herbaceous alien garden species that are regularly traded and planted in Europe according to the European Garden Flora (Cullen *et al.*, 2011; Table 1). These species were selected on the criteria that they are alien to Central Europe and not naturalized there, and are a subset of the species used in Haeuser *et al.* (2017). As garden plants in Central Europe cover a wide range of native climatic origins (Haeuser *et al.*, 2018), the target species were selected to reflect this (Table 1). We characterized species' climatic origins based on median annual average temperatures within their native ranges (for details on how we calculated this metric, see Appendix 1). As competitor resident species, we selected ten native and ten already-naturalized alien species known to occur in grassland communities in Germany (Table 1). All but two competitor species (Table 1) are also present in the European Garden Flora, indicating their common use in European gardens. Although some of the species can grow as annuals or biennials, all of them, with the exception of the naturalized competitor species *Veronica persica*, can grow as perennials (Table 1). Seeds of the 29 study species were bought from B&T World Seeds (Aigues-Vives, France) or Rieger-Hoffman (Blaufelden-Raboldshausen, Germany), or obtained from the seed collection of the Botanical Garden of the University of Konstanz (Table 1).

Pre-cultivation and experimental set-up

Pre-cultivation of seedlings and the experiment were conducted in the greenhouse facilities at the Botanical Garden of the University of Konstanz, Germany (47.69° N, 9.18°E). The average annual temperature and precipitation in Konstanz from 2000-2010 was 9.8°C and 1048.4 mm, respectively (World Weather Online, 2016). Climate models for the German state of Baden-Württemberg, within which Konstanz is located, predict an increase in average annual temperature of over 2.4°C by the end of the century (LUBW, 2013). The climate projections for precipitation are more variable, but most models predict a decrease in summer precipitation and an increase in the number of drought periods (LUBW, 2013).

To obtain seedlings for the experiment, seeds of each of the 29 species were sown in trays (48 x 33 x 6.5 cm; one tray per species) filled with a standard potting soil (Standard, Gebr. Patzer GmbH & Co. KG, Sinntal, Germany) 1-3 weeks before transplanting. The trays were placed in growth chambers with day/night temperatures of 22/18°C, and 10 hours of daylight at 90% humidity. From previous experiments (e.g. Haeuser *et al.*, 2017), we knew that our species vary in the time required for germination. Therefore, to ensure that all species would have comparable sizes at the time of transplanting, slow-germinating species were sown up to two weeks before the fast-germinating species.

Due to the large number of plants, transplanting of the seedlings was conducted over four days from 23-26 November 2015. In 3L pots, each containing a 2:1 mixture of sand and potting soil and 7.5 g of a slow-release fertilizer (2.5g/l Osmocote Exact Standard fertilizer; 3-4 month, 16-9-12+2MgO+TE, Everris GmbH, Nordhorn, Germany), one target plant (i.e. a non-naturalized alien garden plant) was planted in the center of the pot. Five individuals of a single competitor species (i.e. one of the 10 native or the 10 naturalized alien species) were planted in even spacing around the target plant, approximately 6 cm apart from the target plant and from each other. Each target species was grown with each of the 20 competitor species, and also without competitors. We had one replicate for each combination of a target species (n=9) and competitor treatment (n=10+10+1=21) in each of the temperature (n=4) by watering treatment (n=2) combinations (see below). This resulted in a total of 1512 pots. At the time of transplanting, we counted the number of true leaves and measured the length of the longest leaf of each target plant as measures of initial size. For two weeks following initial transplanting, seedlings that had died were replaced with new seedlings, for which we also took new initial size measurements.

Following transplanting, pots were immediately moved to one of four greenhouse compartments each with a different temperature treatment, and placed across three tables within each compartment according to randomly assigned numbers. The control temperature treatment simulated temperatures across a typical growing season in Konstanz, with daily high and low temperatures across the three-month experiment tracking the average Konstanz temperatures for 1 May to 31 July (Fig. S1), according to 2011-2015 average daily minimum and maximum temperatures (NOAA, 2015). The desired temperature regimes were imposed using heating pipes located below the tables as well as at the sides and ceiling of the greenhouse compartments, and with hot air blown into the greenhouse from fabric hoses below the side tables. If cooling was required beyond the cooling achieved by switching off the heating, the roof and side windows were opened or a cooling aggregate was switched on. Temperatures were measured with a ventilated temperature sensor at the height of the plants. The light period was adjusted daily with artificial lighting to approximately match the corresponding day in the season (Fig. S1; timeanddate.com, 2015).

The daily minimum temperature was maintained at a constant value at night. After ‘sunrise’, the temperature increased until the daily maximum temperature was reached and maintained for one hour at midday, after which the temperature gradually decreased again until reaching the daily minimum at ‘sunset’. Similar temperature patterns were used for the remaining three temperature treatments, but with two, four or six degrees added relative to the control temperatures (Fig. S1). At the time of initial transplanting (23 November 2015), all greenhouses were set to their corresponding 1 May conditions, and this was maintained for two weeks until all replacement-transplanting of seedlings that had died was completed, before progression on to 2 May conditions.

One week later (corresponding to 7 May), after all plants had had time to recover from the transplant shock, two water-availability treatments were started: normal and reduced watering. It is difficult to relate watering treatments in greenhouse pot experiments directly to precipitation levels in a natural setting outdoors. However, we aimed for the normally-watered plants in the control temperature treatment to not be water-limited, and for the plants in the highest temperature treatment to not experience high levels of mortality. Pots in the reduced watering treatment were watered half as frequently as the pots in the normal watering treatment. In the first half of the experiment, pots in the normal and reduced watering treatments received

200 ml of water every two and four days, respectively. As daily temperatures increased in each temperature treatment (Fig. S1), greater amounts of water were required to avoid severe plant mortality. In addition, in the current climate of Konstanz, mean monthly precipitation is higher in June and July than in May (World Weather Online, 2016), and so our water-availability treatments reflect current precipitation patterns. Therefore, from experimental day 49 onwards (corresponding to 18 June), we increased watering to 250 ml every day for the normal watering treatment and every two days for the reduced watering treatment. To aid water retention, we also placed saucers underneath the pots. Soil-moisture measurements taken on day 51 showed that soil moisture decreased with temperature treatment ($F_{1, 414.10}$=270.92, p<0.001). Soil moisture was also significantly lower in the reduced watering treatment in all four temperature treatments ($F_{1,459.46}$=264.36, p<0.001), but the difference in soil moisture between the watering treatments decreased with increasing temperatures ($F_{1,460.20}$=123.82, p<0.001; Figure S2).

Measurements

Harvesting of the plants began on day 92 of the experiment (corresponding to 31 July) and was completed in eight days. During this time, temperature and watering treatments were maintained with daily minimum and maximum temperatures held constant at day 92 values. To avoid biases due to different harvesting dates, we harvested equal numbers of pots from each temperature treatment each day. For the target non-naturalized garden plants, we assessed survival, flowering probability (yes, no) and the number of flowers present if flowering, and harvested all aboveground biomass. For native and naturalized competitor plants, we also assessed survival (i.e. the proportion of the five plants per pot that survived) and flowering probability (yes, no for any competitor plants flowering in a pot). Then we harvested the collective aboveground biomass of all competitor plants in a pot. Biomass was dried for at least 72h at 70°C immediately after harvesting and again for at least 24h prior to being weighed.

Statistical analyses

We analysed the effects of the warming, watering and competition treatments on several absolute metrics of target-plant performance: 1) target survival (yes/no), 2) target aboveground biomass, 3) target flowering (yes/no) and 4) number of flowers produced per flowering target plant. To assess effects of warming and watering treatments on absolute competitor performance, we also analysed total competitor aboveground biomass, competitor survival (the proportion of surviving competitor plants per pot) and competitor flowering (yes/no). Finally, to measure the performance of target species relative to competitors, we calculated the ratio of target aboveground biomass to the total (target + competitor) aboveground biomass per pot. This is a commonly used metric to quantify the competitive balance between species (e.g. Parepa *et al.*, 2013). Although the effects of the treatments on the target plants and competitors are not independent, as the measured plants grew in the same pots, analysing the effects of the treatments on absolute performance of the competitors provides insight into the possible reasons behind any target responses to the treatments.

The absolute and relative plant-performance metrics were analyzed using generalized linear mixed models (GLMM) with binomial distributions for survival and flowering probability, and linear mixed models (LMM) for the biomass variables. For the subset of flowering target plants, we first analysed the number of flowers in a GLMM with a Poisson distribution, but as these models did not converge, we used a LMM instead. Target biomass and number of flowers were natural-log transformed prior to analysis to improve normality and homoscedasticity of the residuals. All models included as explanatory variables temperature (as a continuous variable), watering treatment (normal or reduced), the competitor species type (native or naturalized), and all two- and three-way interactions between these variables. Because each of the four temperature regimes could only be imposed on an entire greenhouse compartment, we did not have replicate greenhouse compartments for each temperature level. To avoid that the results would suffer from pseudo-replication (Colgrave & Ruxton, 2017), we did not fit temperature as a factor with four levels, which would use up all three degrees of freedom, but instead included it as a continuous covariate, which used up only one of the three degrees of freedom. This allowed us to also account for non-independence of the plants within each greenhouse compartment by additionally including greenhouse compartment as a random factor. Our experimental design in essence reflects a split-plot design, which is frequently used when a certain treatment can only be applied to larger units and one is mainly interested in how this treatment interacts with factors imposed to smaller units (in our case: watering treatment and competitor type) rather than the main effect itself (in our case: temperature; Altman & Krzywinski, 2015).

For metrics assessing target plant performance, we also included target plant climatic origin (continuous variable), and all of its two-, three- and four-way interactions with the other variables. For the analyses of the absolute measures of performance of the target plants (i.e. target survival, aboveground biomass, flowering and number of flowers), we also had pots without competitors, resulting in three competition treatments: no competition, competition with natives, competition with naturalized aliens. To separate between the effects of the presence of competition (yes/no) and competitor type (native or naturalized), we coded them as two separate dummy variables, each with two levels (Schielzeth, 2010), and fitted competition before competitor species type. For the analyses of the target:total biomass ratio per pot and all measures of competitor performance, we excluded the pots in the treatment without competitors. To account for differences in the initial size of the target plants, we fitted initial size (length of longest leaf x number of leaves) as a covariate in models assessing target species performance metrics. To facilitate the interpretation of the model estimates, all continuous variables (temperature, climatic origin, initial size) were standardized to a mean of zero and a standard deviation of one (Schielzeth, 2010). The identities of the target and competitor species were included as random effects, in addition to the random effect of greenhouse compartment. As there was heteroscedasticity in the variance of the target species, we included a weighted variance structure for target species in all LMMs (Table S1). All analyses were conducted in R (R Core Team, 2017). Due to the need to include the weighted variance structure for target species, we used the *nlme* package (Pinheiro *et al.*, 2017) for the LMMs, whereas we used the *lme4* package (Bates *et al.*, 2015) for the GLMMs. We assessed significance of the fixed terms of each model with likelihood-ratio tests (LRTs) comparing the deviance of the complete model and a model from which the fixed term of interest has been removed (Zuur et al. 2009). To aid interpretation of results, we include in the supplementary material outputs of models retaining those terms identified as significant according to the LRTs (Tables S2, S3 & S4).

Results

Absolute performance of non-naturalized alien garden plants

Of the 1521 target individuals (i.e. non-naturalized alien garden plants) planted, 1107 (73.2%) survived until the end of the experiment. Overall target-plant survival was not significantly affected by watering and temperature treatments, and also not by competitor species type and target-plant climatic origin. No interactions between predictor variables were significant.

Aboveground biomass of target plants was significantly affected by temperature according to log-likelihood ratio tests (Table 2). This was, however, limited to plants receiving normal watering, for which biomass increased with increasing temperature (Table S2, Fig. 1a). Under reduced watering, target biomass was unaffected across the temperature gradient (indicated by significant temperature × watering interactions in LRTs and model outputs; Table 2, Table S2, Fig. 1a). Nevertheless, target biomass was lower under reduced watering overall (Table S2). Competition had on average a negative effect on target-plant biomass, and this effect was stronger when the competitors were naturalized aliens instead of natives (Table 2, Table S2, Fig. 1b). There was a significant three-way interaction between temperature, competitor type and climatic origin (Table 2, Table S2), where target species from warmer climatic origins performed worse against naturalized competitors under colder temperature treatments (Fig S3a), but this effect was very weak compared to the main effects acting on target aboveground biomass (Fig. S3a).

Of the 1107 surviving target plants, 498 individuals (45.0%) flowered during the experiment. While the probability of flowering was lower under reduced watering was somewhat higher when targets were grown without competition, it was lower when they were grown in competition with resident species (indicated by a significant watering × competition interaction; Table 2, Table S2, Fig. 1c). Flowering probability was lower under higher temperatures for target plants grown with naturalized competitors, more so than for those grown with native competitors (significant temperature × competitor type interaction; Table 2, Table S2, Fig. 1d). The species from warmer climatic origins were somewhat less likely to flower when temperatures increased (significant temperature × climatic origin interaction; Table 2, Table S2, Fig. S3b). Species from warmer climatic origins were also less likely to flower when grown with naturalized competitors compared to native ones (significant climatic origin × competitor type interaction, Table 2, Table S2, Fig. S3c), but both of these effects were rather weak (Fig. S3b, c). Among the flowering target plants, the number of flowers per plant did not vary with temperature for those grown in competition with naturalized species, but at higher temperatures, flower number was higher for target plants grown in competition with naturalized species compared to native ones (indicated by a significant temperature x competitor type interaction, Table 2, Table S2, Fig. 1d). The number of flowers produced by target plants varied across different climatic origins, depending on the watering treatment (indicated by a significant watering × climatic origin interaction, Table 2, Table S2). However, this variation did not show strong directional trends (Fig. S3d).

Absolute performance of competitors

Competitor species survival was high, with an average of 4.60 (SE=0.02) out of 5 plants surviving in each pot. We found no significant effects for temperature, watering treatment or competitor type (Table 3). However, naturalized competitors performed worse at higher temperatures compared to native competitors in terms of survival (significant temperature × competitor type interaction; Table 3, Table S3, Fig. 2a.). In addition, survival was lower at higher temperatures when watering was also reduced compared to normal levels (significant temperature × watering interaction; Table 3, Table S3, Fig. 2b).

Aboveground biomass of the competitors was significantly lower under higher temperatures and reduced watering (Table 3, Table S3), and especially so when both were combined (significant temperature × watering interaction; Table 3, Table S3, Fig. 2c). Biomass was significantly higher for naturalized than for native competitors, but this difference was reduced at higher temperatures (significant temperature × competitor type interaction; Table 3, Table S3, Fig. 2d) as well as under reduced watering (significant watering x competitor type interaction; Table 3, Table S3, Fig. 2e).

Of the 1440 pots with competitors, 735 (51.0%) had at least one flowering competitor plant. Flowering probability of the competitors decreased significantly with increasing temperatures (Table 3, Table S3, Fig. 2f). Flowering did not differ between watering treatments, nor competitor types (Table 3).

Performance of non-naturalized alien garden plants relative to competitors

The ratio of target biomass to total biomass per pot increased with increasing temperature (Table 4, Table S4, Fig. 3a), as target biomass increased (Table 2, Fig. 1a) and competitor biomass decreased (Table 3, Fig. 2a). The target:total biomass ratio was also marginally higher under reduced watering than under normal watering (Table 4, Table S4, Fig. 3b). Moreover, this ratio was higher in pots with native competitors compared to naturalized ones (Table 4, Table S4, Fig. 3c). There was a significant interaction between the effects of climatic origin and competitor type (Table 4, Fig. S3e). Target plants with warmer climatic origins performed slightly worse against naturalized competitors compared to those from colder climatic origins (Table S4). However, this effect was weak relative to the main effects acting on biomass ratio.

Discussion

In our experiment, non-naturalized herbaceous alien garden plants responded to simulated changes in climate in ways that clearly differed from how the herbaceous native and naturalized resident species responded. Whereas non-naturalized alien species were relatively tolerant or even improved performance, resident species responded negatively to increased temperatures and reduced watering (Fig. S4). Naturalized resident species were more competitive against the non-naturalized alien species than the native resident species were overall, but the performance of both competitor types declined under simulated climate changes. This suggests that under climate change, some resident communities, at least common grassland communities in Central Europe, will become more susceptible invasion by novel alien plants. So, many currently non-naturalized alien garden species will be well positioned to establish naturalized populations and potentially become invasive.

Climate-change effects on performance of non-naturalized alien garden plants and residents

Whereas survival of the non-naturalized alien garden plants was largely unaffected by temperature and water availability (Table 2), survival of the resident competitors was (Table 3, Fig. 2a, b). Survival of resident competitors was reduced in the highest temperature treatment, and this was exacerbated by reduced water availability. Increased precipitation, and thus a high water availability, has been predicted for some regions of the world (IPCC, 2014), and has been linked to increased invasion success (Dukes & Mooney, 1999; Blumenthal *et al.*, 2007; but see Liu *et al.*, 2017). Our results suggest that reduced precipitation, and thus reduced water availability, will lead to less competition from the resident community and that this may facilitate the naturalization of new, more drought-tolerant alien species. In line with the findings of this study, Haeuser *et al.* (2017) recently found that non-naturalized alien species established from seed were more tolerant of climate warming than native species. On the other hand, Haeuser *et al.* (2017) also found that the non-naturalized alien species had lower survival after one season under increased temperatures. We did not find reduced survival here, possibly due to our focus on a different life stage (i.e. planted seedlings). Fay & Schultz (2009) noted that while species differ in responses to precipitation variability, established seedlings tend to be more tolerant of variability in precipitation than germinating seeds. Nonetheless, our results show that future altered climates (increased temperatures and reduced water availability) will likely favour seedling survival of multiple non-naturalised garden plants over resident species.

Aboveground biomass increased with temperature for non-naturalized species whereas it decreased for resident competitors. Consequently, the ratio of target to total aboveground biomass per pot — a measure of competitive balance (e.g. Parepa *et al.* (2013) — increased with temperature. In addition, although biomass of the non-naturalized species decreased with reduced water availability, especially at higher temperatures, the negative effect of this treatment on biomass of resident species was even greater. As a consequence, the ratio of target to total aboveground biomass per pot still increased—albeit to a lesser degree—with reduced water availability. These findings suggest a competitive advantage for the non-naturalized species under increased temperatures and drought. Alternatively, it could be that the native and naturalized alien competitors had a stronger shift of biomass allocation towards belowground tissues, which we could not measure, than the non-naturalized alien species, resulting in higher ratios of the target to total aboveground biomass per pot. Plants usually allocate more biomass to their roots when water availability is reduced (e.g. Fay *et al.*, 2003; Quezada & Gianoli, 2010), and there is some evidence that naturalized alien plant species have higher shoot-mass fractions than native plants (e.g. Wilsey & Polley, 2006, van Kleunen *et al.*, 2010; Kuebbing *et al.*, 2015). However, it is not known whether this also applies to non-naturalized alien plants. Most importantly, we do not know if the three groups of species differ in plastic shoot-mass fraction responses to warming and reduced water availability. Moreover, we note that differing responses in germination and phenology may also affect the competitive abilities of alien and resident species, but these effects were outside the scope of this study. Nevertheless, if aboveground biomass is representative of total biomass, our findings indicate that under a projected warmer climate with more summer drought events in Germany (IPCC, 2014), many currently non-naturalized herbaceous alien garden plants may gain a competitive advantage over the current native and naturalized alien residents.

Effects of climate-change treatments on the probability of flowering and number of flowers produced by non-naturalized alien garden plants were somewhat negative (Fig. 1c, d, e). However, those effects were weak compared to the negative response of competitor flowering to temperature increases (Fig. 2f). This suggests that the non-naturalized aliens in our study are not only more successful than resident species at the vegetative growth stage but also at the flowering stage. Still, as the majority of species in our study are perennial species, it could be that some species under more stressful conditions opted to delay reproduction until later in the season (e.g. Llorens & Peñuelas, 2005) or until a later growing season. Therefore, further work is required to assess whether the observed relatively high flowering success of non-naturalised aliens over resident species will translate into higher reproductive output under climate change.

Responses and effects of differing resident competitor types

Naturalized competitors had more aboveground biomass than native competitors across the different temperature and watering treatments. As the competitors were always grown in competition with the target plants, this biomass difference could indicate that the native species are more sensitive to competition. However, as previous studies have shown that naturalized or invasive species often are larger or have higher growth rates than native species (Grotkopp & Rejmánek 2007; van Kleunen *et al.* 2010), the biomass difference may indicate an inherently larger size of the naturalized compared to the native species in our study. Under reduced water availability, however, this difference was reduced. Moreover, survival decreased more strongly at the highest temperatures for naturalized species than for native species. This contradicts the idea that naturalized species should be more resilient to climate change, due to broader climatic niches (Leiblein-Wild *et al.*, 2014), selective introduction of more plastic genotypes, (Bossdorf *et al.*, 2008), or a greater ability to adjust their phenology to track climate change compared to native species (Willis *et al.*, 2010). In a recent meta-analysis, Liu *et al.* (2017) found that invasive species benefited more than native species from increased temperatures and CO_2 concentrations, but that invasive species were somewhat less tolerant to reduced precipitation. The latter trend was also reported in another meta-analysis (Sorte *et al.*, 2012), and is in line with our findings. In regions such as Germany, where precipitation variability is projected to increase and drought periods are likely to become more frequent (IPCC, 2014), the performance of currently naturalized alien species may therefore be reduced.

Interestingly, across temperature and watering treatments, non-naturalized alien target species tended to perform worse when in competition with naturalized species than with native species. Possibly this is a consequence of the naturalized species being larger than the native species, and that they therefore have a stronger competitive effect (Dostál, 2011). Nevertheless, this suggests that the naturalized species may retain a competitive advantage over native species under climate change, and could possibly resist new alien species incursions better than the native species. This may mean that under a warmer, drier climate, establishment of currently non-naturalized alien species is less likely to be facilitated by already-naturalized alien species (‘invasion meltdown’; Simberloff & Von Holle 1999), at least among plant species. Kuebbing & Nuñez (2016), however, found evidence that non-native species can facilitate new alien establishment even when interactions between non-native species are negative. Nevertheless, as our results indicate that both resident groups will perform worse under climate change, it is likely that they will be out-competed by newly-naturalizing species better suited to the new climates.

Variation in climate-change responses among non-naturalized alien plant species

The non-naturalized alien species used in this study were selected because they are not currently naturalized in Central Europe, and because they cover different climatic origins. One of them, *Persicaria capitata*, is already naturalized in the Mediterranean, and another, *Verbena rigida*, is naturalized on the Azores and Madeira (http://www.europe-aliens.org, accessed 6 February 2018). Furthermore, all of these species except *Eritrichium canum*, have naturalization records outside of Europe, usually in warmer parts of the world (Table S5). Thus, many non-naturalized alien species that are currently grown in Central European gardens have naturalization potential, particularly in warmer climates. The variation in performance measures and responses to the climate-change treatments among the non-naturalized alien species was only weakly and not consistently related to the climatic origins of the species (Fig. S3). In a previous study that also included an overwintering period, we found that climatic origin (i.e. winter hardiness) improved colonization ability and that this effect became weaker in heated plots (Haeuser *et al.*, 2017). In the current study, the majority of our target species exhibited positive or no responses to warming overall, regardless of climatic origin. If winter hardiness, however, becomes less limiting for species from warmer climates, naturalization risk of these species will increase. This risk will likely be exacerbated if species from warmer climates are then also introduced and planted in greater numbers in our gardens (Bradley *et al.*, 2012). At the same time, the naturalization risk from species more suited to current climates in Germany may not necessarily diminish. Rather than experiencing a turnover of alien invaders due to climate change, Germany's pool of potential invaders may simply increase.

Interactions between climate-change components

We tested how temperature-driven soil moisture reduction is exacerbated by a simultaneous reduction in precipitation, which mirrors the climatic changes expected for summers in southern Germany (LUBW, 2013; IPCC, 2014). Because soil moisture inherently decreases with increased temperature due to increased evapotranspiration, it is not possible to fully separate the effects of temperature and water availability. In a previous study testing the effects of climate warming, we also found that heating resulted in decreased water availability even under uniform precipitation (Haeuser *et al.*, 2017). Therefore, a significant portion of the effects of temperature may be mediated by changes in soil moisture. De Boeck *et al.* (2011) showed that heat waves (our +6° C treatment might be representative for such a heatwave) had few negative effects on plant community performance when there was sufficient water available. Nevertheless, temperature increases may also have direct impacts on plant performance. Temperature increases have been shown to benefit invaders through the promotion of growth, stress tolerance and canopy cover (He *et al.*, 2012), or through the advancement of their phenology (Chuine *et al.*, 2012). Other global-change components, such as increases in atmospheric CO_2 levels, will also likely interact with rising temperatures and changing precipitation to affect species to differing degrees (Long, 1991; Alberto *et al.*, 1996; Farquhar, 1997; Weltzin *et al.*, 2003). Thus, more studies including alien garden and resident species and different global-change components are required to understand how interactions between global change components affect naturalisation risk.

Conclusions

Our findings demonstrate the need to study climate-change components in concert, as their effects in isolation may differ from those resulting from their interactions. Non-naturalized alien garden plants exhibited improved or stable performance under increasing temperature and reduced water availability in terms of survival and vegetative growth, although flowering was somewhat negatively affected by increased temperatures and reduced water availability. Resident species, on the other hand, performed generally worse under increasing temperatures and reduced water availability, although naturalized resident species performed better than native species overall. The weak effects of climatic origin on performance responses of non-naturalized alien garden species to climate change suggest that the pool of potential invaders in Germany will not be limited to species originating in climatically-comparable regions. At a local community scale, the improved performance of the aliens and decreased performance of the residents suggests that competition will decrease with climate change, offering more opportunities for the establishment of more tolerant alien garden species. We can therefore expect more naturalizations of alien garden plant species under future climate change.

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Data accessibility

Data available from the Dryad Digital Repository: (Haeuser, Dawson & van Kleunen 2018).

Author Contributions

EH, MvK and WD designed the study. EH implemented the study, collected the data, did the analyses with inputs from MvK and WD, and wrote the manuscript with the help of MvK and WD.

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Table 1: Target and competitor species used in the experiment. Climatic origin indicates median annual mean temperature within a species' native range (see Appendix 1). Life span indicates the typical life span of the species. Native continents indicate continents to which the species are native. Supplier indicates seed source: B&T World Seeds (B&T; Aigues-Vives, France), Rieger-Hoffman (R.H.; Blaufelden-Raboldshausen, Germany), or University of Konstanz Botanical Garden (U.K.; Konstanz, Germany). EGF indicates whether or not the species is listed in the European Garden Flora (Cullen *et al*., 2011).

Species	**Species type**	**Type**	**Climatic origin**	**Life span**	**Native continent(s)**	**Supplier**	**EGF**
Eritrichium canum	Target	Non-naturalized alien	-2.41	Annual/perennial	Asia	B&T	Yes
Gilia tricolor	Target	Non-naturalized alien	15.50	Annual/perennial	N. America	B&T	Yes
Iris domestica	Target	Non-naturalized alien	15.99	Perennial	Asia	B&T	Yes
Monarda fistulosa	Target	Non-naturalized alien	9.64	Perennial	N. America	B&T	Yes
Monarda punctata	Target	Non-naturalized alien	14.18	Perennial	N. America	B&T	Yes
Persicaria capitata	Target	Non-naturalized alien	14.94	Perennial	Asia	B&T	Yes
Platycodon grandiflorus	Target	Non-naturalized alien	4.06	Perennial	Asia	B&T	Yes
Rudbeckia triloba	Target	Non-naturalized alien	12.31	Perennial	N. America	B&T	Yes
Verbena rigida	Target	Non-naturalized alien	19.18	Perennial	S. America	B&T	Yes
Achillea millefolium	Competitor	Native	6.40	Perennial	Asia, Europe, N. America	R.H.	Yes
Allium schoenoprasum	Competitor	Native	7.49	Perennial	Asia, Europe, N. America	R.H.	Yes
Leontodon autumnalis	Competitor	Native	3.14	Perennial	Asia, Europe, N. America	R.H.	Yes
Leucanthemum vulgare	Competitor	Native	6.15	Perennial	Asia, Europe	R.H.	Yes
Lotus corniculatus	Competitor	Native	8.30	Perennial	Africa, Asia, Europe	R.H.	Yes
Silene dioica	Competitor	Native	4.93	Biennial/perennial	Europe	R.H.	Yes
Silene flos-cuculi	Competitor	Native	8.32	Perennial	Europe	R.H.	Yes
Silene vulgaris	Competitor	Native	9.12	Perennial	Europe	R.H.	Yes
Trifolium pratense	Competitor	Native	7.35	Biennial/perennial	Africa, Asia, Europe	R.H.	Yes
Viola tricolor	Competitor	Native	7.58	Perennial	Europe	R.H.	Yes
Antirrhinum majus	Competitor	Naturalized alien	13.54	Annual/perennial	so. Europe	B&T	Yes
Cerastium tomentosum	Competitor	Naturalized alien	10.09	Perennial	Asia, so. Europe	B&T	Yes
Diplotaxis tenuifolia	Competitor	Naturalized alien	13.34	Perennial	Africa, Asia, so. Europe	U.K.	No
Epilobium ciliatum	Competitor	Naturalized alien	6.93	Perennial	Asia, N. America, S. America	U.K.	No
Hesperis matronalis	Competitor	Naturalized alien	10.29	Biennial/perennial	so. Europe	B&T	Yes
Lupinus polyphyllus	Competitor	Naturalized alien	6.73	Perennial	N. America	U.K.	Yes
Mimulus guttatus	Competitor	Naturalized alien	8.25	Annual/perennial	N. America	U.K.	Yes
Oenothera biennis	Competitor	Naturalized alien	9.00	Biennial/perennial	N. America	U.K.	Yes
Solidago gigantea	Competitor	Naturalized alien	8.91	Perennial	N. America	U.K.	Yes
Veronica persica	Competitor	Naturalized alien	13.61	Annual	Asia, so. Europe	U.K.	Yes

Table 2: Results of generalized linear mixed-models (survival, flowering) and linear mixed models (aboveground biomass, flower number) testing the significance of the effects of climate treatments (temperature, watering), competition (yes, no), competitor type (native, naturalized), target species climatic origin effects, their interactions, and initial target plant size on performance measures of the target species. Significant (P < 0.05) effects are indicated in bold.

			Survival		**Aboveground biomass**		**Flowering**		**Flower number**	
Fixed Effects	**Order[†]**	**df**	**LRT***	**P**	**LRT***	**P**	**LRT***	**P**	**LRT***	**P**
Initial size	5	1	0.010	0.921	3.007	0.083	0.993	0.319	0.004	0.947
Climatic origin	4	1	1.683	0.195	0.152	0.697	0.664	0.415	0.287	0.592
Temperature	4	1	0.438	0.508	**20.882**	**<0.001**	1.972	0.160	1.617	0.204
Watering	4	1	3.104	*0.078*	**18.758**	**<0.001**	**13.172**	**<0.001**	3.621	0.057
Competition (Y/N) [§]	4B	1	2.624	0.105	**4.750**	**0.029**	**5.301**	**0.021**	3.015	0.083
Competitor type	4A	1	0.099	0.753	**4.560**	**0.033**	**4.842**	**0.028**	0.608	0.436
Temperature:Watering	3	1	2.227	0.136	**4.709**	**0.030**	1.144	0.285	3.557	0.059
Temperature:Competition	3B	1	0.072	0.788	0.710	0.400	0.196	0.658	1.114	0.291
Temperature:Competitor type	3A	1	0.912	0.340	0.176	0.674	**4.824**	**0.028**	**5.404**	**0.020**
Watering:Competition	3B	1	1.066	0.302	0.030	0.853	**5.710**	**0.017**	0.056	0.813
Watering:Competitor type	3A	1	0.559	0.455	0.020	0.865	1.118	0.290	0.002	0.960
Climatic origin:Temperature	3	1	0.356	0.551	1.190	0.275	**11.899**	**0.001**	2.794	0.095
Climatic origin:Watering	3	1	0.048	0.827	0.027	0.867	0.007	0.932	**9.015**	**0.003**
Climatic origin:Competition	3B	1	1.846	0.174	1.472	0.225	0.133	0.716	0.121	0.728
Climatic origin:Competitor type	3A	1	1.037	0.308	**41.070**	**<0.001**	**12.691**	**<0.001**	1.942	0.164
Temperature:Watering:Competition	2B	1	0.126	0.723	0.086	0.770	0.429	0.513	0.902	0.342
Temperature:Watering:Competitor type	2A	1	0.181	0.671	1.816	0.178	1.755	0.185	0.229	0.632
Climatic origin:Temperature:Watering	2	1	0.035	0.851	0.477	0.490	0.759	0.384	1.325	0.250
Climatic origin:Temperature:Competition	2B	1	0.336	0.562	0.439	0.507	0.004	0.948	0.510	0.475
Climatic origin:Temperature:Competitor type	2A	1	0.041	0.839	**6.697**	**0.010**	0.016	0.901	0.066	0.797
Climatic origin:Watering:Competition	2B	1	1.823	0.177	0.111	0.739	1.738	0.187	0.853	0.356
Climatic origin:Watering:Competitor type	2A	1	0.050	0.824	1.120	0.290	0.181	0.670	1.133	0.287
Climatic origin:Temperature:Watering:Competition	1B	1	1.488	0.223	0.308	0.579	0.502	0.479	0.035	0.852
Climatic origin:Temperature:Watering:Competitor type	1A	1	0.010	0.921	0.018	0.893	0.033	0.855	0.272	0.602
Random effects			**Std.Dev.**	**Levels**	**Std.Dev.**	**Levels**	**Std.Dev.**	**Levels**	**Std.Dev.**	**Levels**
Target species[‡]			1.512	9	1.094	9	2.982	9	1.828	9
Competitor species			0.535	21	0.672	21	0.997	21	0.460	21
Greenhouse			0.100	4	0.001	4	0.077	4	0.002	4
Number observations:				1512		1103		1104		497

*Significances of the fixed terms were tested using log-likelihood ratio tests (LRT) comparing models with and without the term of interest.

[†] Order indicates the sequence in which fixed terms were removed from the model for LRTs.

[§] For competition (no competition, competition with native, competition with naturalized species), we created two dummy variables to contrast no competition vs. competition and native vs. naturalized competitors. As the latter are nested within the with-competition treatment, competitor type terms (order A) were always removed before corresponding competition terms (order B).

[‡] Standard deviations for individual target species random effects for the saturated model are found in Table S1.

Table 3: Results of generalized linear mixed-models (survival, flowering) and a linear mixed model (aboveground biomass) testing the significance of the effects of climate treatments (temperature and watering), competitor type (native or naturalized) and their interactions on performance measures of competitor plants, i.e. proportion competitors surviving, total competitor aboveground biomass, and competitor flowering probability (yes, no). Significant (p < 0.05) effects are indicated in bold.

			Survival		**Aboveground biomass**		**Flowering**	
Fixed Effects	**Order[†]**	**df**	**LRT***	**P**	**LRT***	**P**	**LRT***	**P**
Temperature	3	1	3.208	0.073	**9.621**	**0.002**	**6.158**	**0.013**
Watering	3	1	3.746	0.053	**185.299**	**<0.001**	1.015	0.314
Competitor type	3	1	0.074	0.786	**110.207**	**<0.001**	0.092	0.762
Temperature:Watering	2	1	**12.312**	**<0.001**	**50.609**	**<0.001**	0.525	0.469
Temperature:Competitor type	2	1	**16.342**	**<0.001**	**4.433**	**0.035**	0.048	0.827
Watering:Competitor type	2	1	0.174	0.676	**38.275**	**<0.001**	0.018	0.894
Temperature:Watering:Competitor type	1	1	0.456	0.499	0.034	0.854	0.687	0.407
Random effects			**Std. Dev.**	**Levels**	**Std. Dev.**	**Levels**	**Std. Dev.**	**Levels**
Target species[‡]			0.232	9	1.741	9	<0.001	9
Competitor species			0.986	20	4.478	20	2.98	20
Greenhouse			0.254	4	0.009	4	0.116	4
Number observations:				1431		1436		1427

*Significances of the fixed terms were tested using log-likelihood ratio tests (LRT) comparing models with and without the term of interest.

[†] Order indicates the sequence in which fixed terms were removed from the model for LRTs.

[‡] Standard deviations for individual target species random effects for the saturated model are found in Table S1.

Table 4: Results of a linear mixed model testing the significance of the effects of treatments (temperature and watering), competitor type and their interactions on the ratio of target aboveground biomass to total aboveground biomass per pot. Significances of the fixed terms were tested using log-likelihood ratio tests (LRT) comparing models with and without the term of interest. Order indicates the sequence in which fixed terms were removed from the model for LRTs. Significant ($p < 0.05$) effects are indicated in bold. Standard deviations for individual target species random effects for the saturated model are found in Table S1.

			Target:total biomass ratio	
Fixed Effects	**Order**	**df**	**LRT**	**P**
Initial size	5	1	**28.244**	**<.0001**
Climatic origin	4	1	3.666	0.056
Temperature	4	1	**32.322**	**<.0001**
Watering	4	1	3.730	0.053
Competitor type	4	1	**94.932**	**<.0001**
Temperature:Watering	3	1	0.045	0.832
Temperature:Competitor type	3	1	0.922	0.337
Watering:Competitor type	3	1	1.006	0.316
Climatic origin:Temperature	3	1	0.011	0.916
Climatic origin:Watering	3	1	0.159	0.691
Climatic origin:Competitor type	3	1	**4.827**	**0.028**
Temperature:Watering:Competitor type	2	1	0.000	0.993
Climatic origin:Temperature:Watering	2	1	0.495	0.482
Climatic origin:Temperature:Competitor type	2	1	1.865	0.172
Climatic origin:Watering:Competitor type	2	1	0.556	0.456
Climatic origin:Temperature:Watering:Competitor type	1	1	0.174	0.676
Random effects			**Std. Dev.**	**Levels**
Target species			<0.001	9
Competitor species			<0.001	20
Greenhouse			<0.001	4
Number observations:				1096

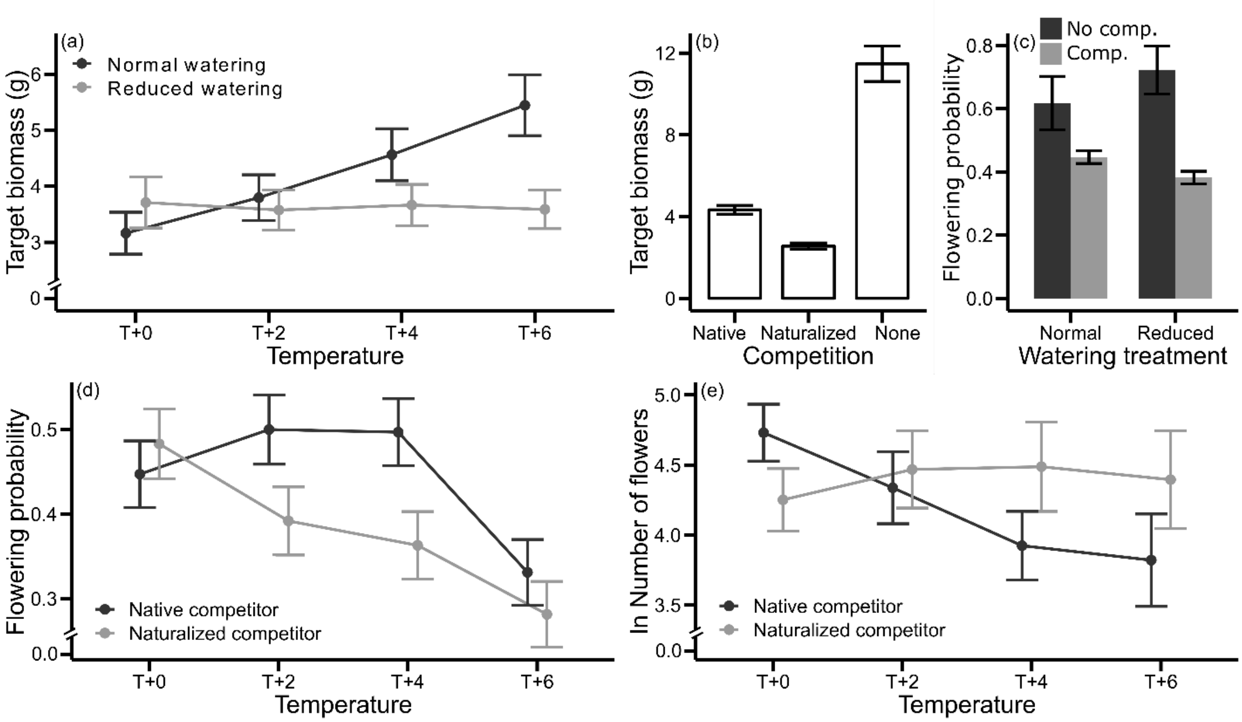

Figure 1: Target plant performance in terms of aboveground biomass (a, b), flowering (yes, no; c, d) and number of flowers (in the case of flowering, and natural-log transformed; e) in response to temperature (a, d, e) and watering (a, d) treatments, and across competition types (b, c, d, e). Error bars indicate standard errors.

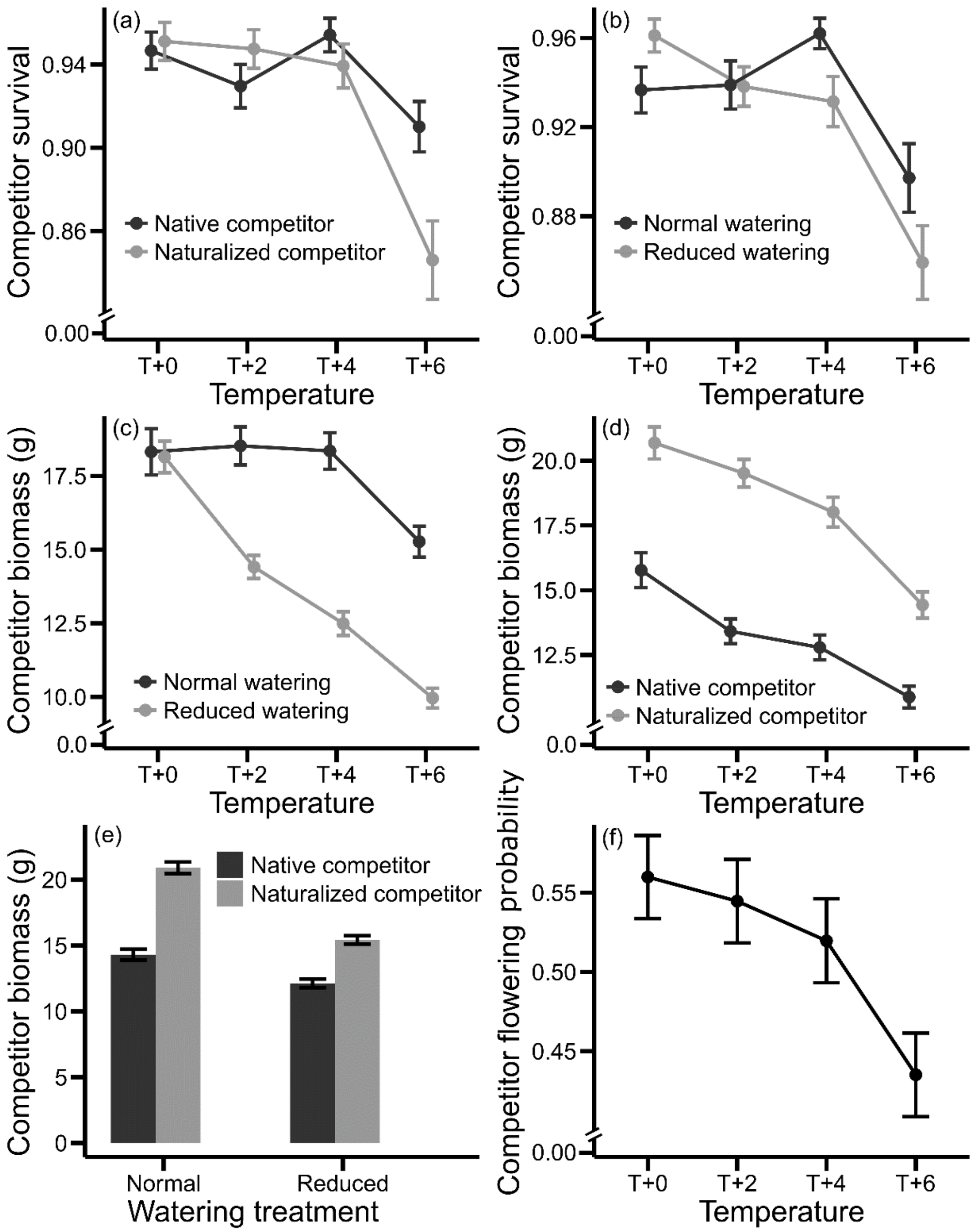

Figure 2: Competitor plant performance in terms of survival (proportion of plants surviving; a, b), aboveground biomass (c, d, e) and flowering probability of any competitor plants (yes, no; f) in response to temperature (a, b, c, d, f) and watering (b, c, e) treatments, for native and naturalized competitors (a, d, e). Error bars indicate standard errors.

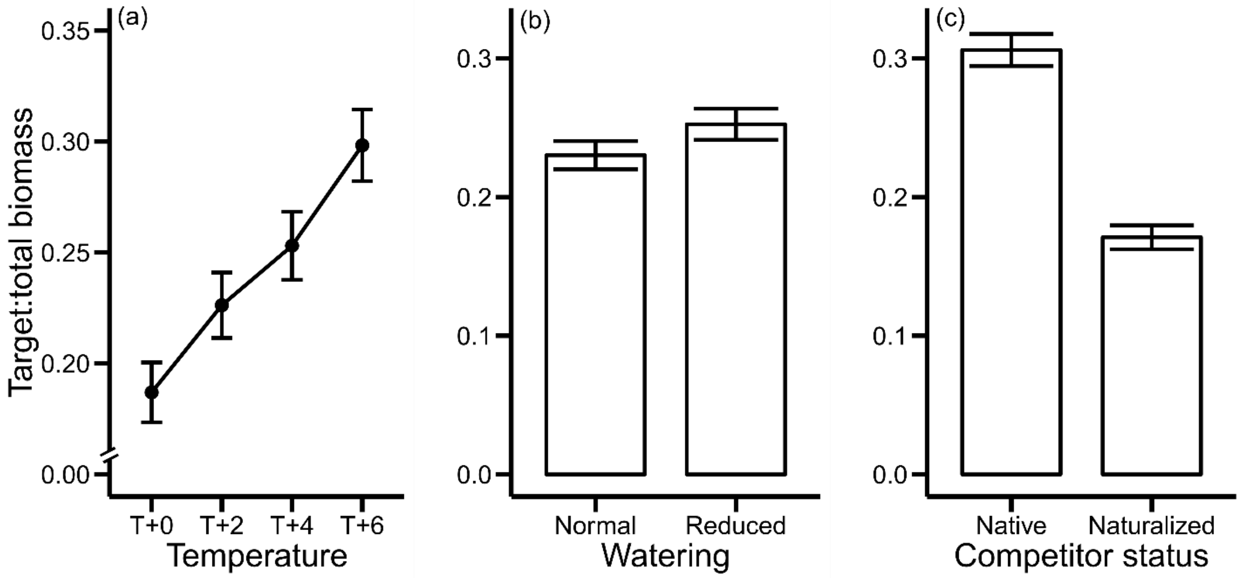

Figure 3: Ratio of target plant aboveground biomass to total aboveground biomass per pot across temperature treatments (a), under different watering regimes (b), and against native vs. naturalized competitors (c). Error bars indicate standard errors.

List of Supporting Information

Appendix 1: Species climatic origin calculations.

Table S1: Standard deviations for individual target species random effects.

Table S2: Estimate outputs for absolute target performance models.

Table S3: Estimate outputs for absolute competitor performance models.

Table S4: Estimate outputs for relative target performance model.

Table S5: Global naturalization records for target species.

Table S6: Reference information for data used to calculate climatic origins

Figure S1: Experimental growing season simulation, including temperature treatment.

Figure S2: Differences in soil moisture levels across treatments.

Figure S3: Effects of climatic origin on absolute and relative target species performance.

Figure S4: Target and competitor responses to climate change treatments.