

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

KEYWORDS

biological invasions, climate change, competition, drought, garden plants, invasion debt, non-native plants, ornamental species

1 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, Galatowitsch, & Gomez, 2006; Chrobock, Kempel, Fischer, & van Kleunen, 2011; Kitajima, Fox, Sato, & Nagamatsu, 2006; Maurel, Hanspach, Kühn, Pysek, & van Kleunen, 2016; Moodley, Geerts, Richardson, & Wilson, 2013; Pemberton & Liu, 2009; Trusty, Lockaby, Zipperer, &

Goertzen, 2008). 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, Dawson, & van Kleunen, 2017; Mayer et al., 2017). As many alien garden plants in temperate regions come from warmer, low-latitude regions (Van der Veken, Hermy, Vellend, Knapen, & Verheyen, 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, Early, & Bellemare, 2013). It has been suggested that some recent naturalization events have been triggered by climate change (Bellemare & Deeg, 2015; Walther et al., 2007). 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., Liu et al., 2017; Manea, Sloane, & Leishman, 2016; Pattison & Mack, 2008), but their focus is typically limited to individual climatic components (e.g., Frei, Ghazoul, Matter, Heggli, & Pluess, 2014; Haeuser et al., 2017; Schrama & Bardgett, 2016). 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, Blumenthal, Wilcove, & Ziska, 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, Dawson, Bossdorf, & Fischer, 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, Urban, Tewksbury, Gilchrist, & Holt, 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 (Pyšek et al., 2017; van Kleunen et al., 2015). 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: (a) 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? (b) 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? (c) 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?

2 MATERIALS AND METHODS

2.1 Study species and precultivation

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, Knees, Cubey, & Shaw, 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,

TABLE 1 Target and competitor species used in the experiment. Climatic origin indicates median annual mean temperature within a species' native range (see Supporting Information Appendix S1). 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
<i>Eritrichium canum</i>	Target	Non-naturalized alien	-2.41	Annual/ perennial	Asia	B&T	Yes
<i>Gilia tricolor</i>	Target	Non-naturalized alien	15.50	Annual/ perennial	N. America	B&T	Yes
<i>Iris domestica</i>	Target	Non-naturalized alien	15.99	Perennial	Asia	B&T	Yes
<i>Monarda fistulosa</i>	Target	Non-naturalized alien	9.64	Perennial	N. America	B&T	Yes
<i>Monarda punctata</i>	Target	Non-naturalized alien	14.18	Perennial	N. America	B&T	Yes
<i>Persicaria capitata</i>	Target	Non-naturalized alien	14.94	Perennial	Asia	B&T	Yes
<i>Platycodon grandiflorus</i>	Target	Non-naturalized alien	4.06	Perennial	Asia	B&T	Yes
<i>Rudbeckia triloba</i>	Target	Non-naturalized alien	12.31	Perennial	N. America	B&T	Yes
<i>Verbena rigida</i>	Target	Non-naturalized alien	19.18	Perennial	S. America	B&T	Yes
<i>Achillea millefolium</i>	Competitor	Native	6.40	Perennial	Asia, Europe, N. America	R.H.	Yes
<i>Allium schoenoprasum</i>	Competitor	Native	7.49	Perennial	Asia, Europe, N. America	R.H.	Yes
<i>Leontodon autumnalis</i>	Competitor	Native	3.14	Perennial	Asia, Europe, N. America	R.H.	Yes
<i>Leucanthemum vulgare</i>	Competitor	Native	6.15	Perennial	Asia, Europe	R.H.	Yes
<i>Lotus corniculatus</i>	Competitor	Native	8.30	Perennial	Africa, Asia, Europe	R.H.	Yes
<i>Silene dioica</i>	Competitor	Native	4.93	Biennial/ perennial	Europe	R.H.	Yes
<i>Silene flos-cuculi</i>	Competitor	Native	8.32	Perennial	Europe	R.H.	Yes
<i>Silene vulgaris</i>	Competitor	Native	9.12	Perennial	Europe	R.H.	Yes
<i>Trifolium pratense</i>	Competitor	Native	7.35	Biennial/ perennial	Africa, Asia, Europe	R.H.	Yes
<i>Viola tricolor</i>	Competitor	Native	7.58	Perennial	Europe	R.H.	Yes
<i>Antirrhinum majus</i>	Competitor	Naturalized alien	13.54	Annual/ perennial	so. Europe	B&T	Yes
<i>Cerastium tomentosum</i>	Competitor	Naturalized alien	10.09	Perennial	Asia, so. Europe	B&T	Yes
<i>Diploxys tenuifolia</i>	Competitor	Naturalized alien	13.34	Perennial	Africa, Asia, so. Europe	U.K.	No
<i>Epilobium ciliatum</i>	Competitor	Naturalized alien	6.93	Perennial	Asia, N. America, S. America	U.K.	No
<i>Hesperis matronalis</i>	Competitor	Naturalized alien	10.29	Biennial/ perennial	so. Europe	B&T	Yes
<i>Lupinus polyphyllus</i>	Competitor	Naturalized alien	6.73	Perennial	N. America	U.K.	Yes
<i>Mimulus guttatus</i>	Competitor	Naturalized alien	8.25	Annual/ perennial	N. America	U.K.	Yes
<i>Oenothera biennis</i>	Competitor	Naturalized alien	9.00	Biennial/ perennial	N. America	U.K.	Yes
<i>Solidago gigantea</i>	Competitor	Naturalized alien	8.91	Perennial	N. America	U.K.	Yes
<i>Veronica persica</i>	Competitor	Naturalized alien	13.61	Annual	Asia, so. Europe	U.K.	Yes

Dawson, & van Kleunen, 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 Supporting

Information Appendix S1). 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).

2.2 Precultivation and experimental set-up

Precultivation 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 to 2010 was 9.8°C and 1,048.4 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 × 33 × 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 hr 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 2 weeks before the fast-germinating species.

Due to the large number of plants, transplanting of the seedlings was conducted over 4 days from 23 to 26 November 2015. In 3 L pots, each containing a 2:1 mixture of sand and potting soil and 7.5 g of a slow-release fertilizer (2.5 g/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 centre 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 1,512 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 2 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 3-month experiment tracking the average Konstanz temperatures for 1 May to 31 July (Supporting Information Figure 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 (Supporting Information Figure 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 1 hr 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 2, 4, or 6° added relative to the control temperatures (Supporting Information Figure 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 2 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 2 and 4 days, respectively. As daily temperatures increased in each temperature treatment (Supporting Information Figure 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 2 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 ($F_{1,460,20} = 123.82$, $p < 0.001$; Supporting Information Figure S2).

2.3 Measurements

Harvesting of the plants began on day 92 of the experiment (corresponding to 31 July) and was completed in 8 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 above-ground 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 above-ground biomass of all competitor plants in a pot. Biomass was dried for at least 72 hr at 70°C immediately after harvesting and again for at least 24 hr prior to being weighed.

2.4 Statistical analyses

We analysed the effects of the warming, watering, and competition treatments on several absolute metrics of target-plant performance: (a) target survival (yes/no), (b) target above-ground biomass, (c) target flowering (yes/no), and (d) 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 above-ground 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 above-ground biomass to the total (target + competitor) above-ground biomass per pot. This is a commonly used metric to quantify the competitive balance between species (e.g., Parepa, Fischer, & Bossdorf, 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 analysed 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 nonindependence 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, above-ground 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 \times 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 (Supporting Information 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, Bates, DebRoy, & Sarkar, 2017) for the LMMs, whereas we used the *lme4* package (Bates, Machler, Bolker, & Walker, 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, Ieno, Walker, Saveliev, & Smith, 2009). To aid interpretation of results, we include in the Supporting Information outputs of models retaining those terms identified as significant according to the LRTs (Supporting Information Tables S2–S4).

3 RESULTS

3.1 Absolute performance of non-naturalized alien garden plants

Of the 1,521 target individuals (i.e., non-naturalized alien garden plants) planted, 1,107 (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.

Above-ground 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 (Supporting Information Table S2, Figure 1a). Under reduced watering, target biomass was unaffected across the temperature gradient (indicated by significant temperature \times watering interactions in LRTs and model outputs; Table 2, Supporting Information Table S2, Figure 1a). Nevertheless, target biomass was lower under reduced watering overall (Supporting Information 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, Supporting Information Table S2, Figure 1b). There was a significant three-way interaction between temperature, competitor type, and climatic origin (Table 2, Supporting Information Table S2), where target species from warmer climatic origins performed worse against naturalized competitors under colder temperature treatments (Supporting Information Figure S3a), but this effect was very weak compared to the main effects acting on target above-ground biomass (Supporting Information Figure S3a).

Of the 1,107 surviving target plants, 498 individuals (45.0%) flowered during the experiment. While the probability of flowering 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 \times competition interaction; Table 2, Supporting Information Table S2, Figure 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 \times competitor type interaction; Table 2, Supporting Information Table S2, Figure 1d). The species from warmer climatic origins were somewhat less likely to flower when temperatures increased (significant temperature \times climatic origin interaction; Table 2, Supporting Information Table S2, Supporting Information Figure S3b). Species from warmer climatic origins were also less likely to flower when grown with naturalized competitors compared to native ones (significant climatic origin \times competitor type interaction, Table 2, Supporting Information Table S2, Supporting Information Figure S3c), but both of these effects were rather weak (Supporting Information Figure 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 \times competitor type interaction, Table 2, Supporting Information Table S2, Figure 1d). The number of flowers produced by target plants varied across different climatic origins, depending on the watering treatment (indicated by a significant watering \times climatic origin interaction, Table 2, Supporting Information Table S2). However, this variation did not show strong directional trends (Figure S3d).

3.2 Absolute performance of competitors

Competitor species survival was high, with an average of 4.60 (SE = 0.02) out of five 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 \times competitor type interaction; Table 3, Supporting Information Table S3, Figure 2a). In addition, survival was lower at higher temperatures when watering was also reduced compared to normal levels (significant temperature \times watering interaction; Table 3, Supporting Information Table S3, Figure 2b).

Above-ground biomass of the competitors was significantly lower under higher temperatures and reduced watering (Table 3, Supporting Information Table S3), and especially so when both were combined (significant temperature \times watering interaction; Table 3, Supporting Information Table S3, Figure 2c). Biomass was significantly higher for naturalized than for native competitors, but this difference was reduced at higher temperatures (significant temperature \times competitor type interaction; Table 3, Supporting Information Table S3, Figure 2d) as well as under reduced watering (significant watering \times competitor type interaction; Table 3, Supporting Information Table S3, Figure 2e).

Of the 1,440 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, Supporting Information Table S3, Figure 2f). Flowering did not differ between watering treatments, nor competitor types (Table 3).

TABLE 2 Results of generalized linear mixed-models (survival, flowering) and linear mixed models (above-ground 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

Fixed effects	Order ^a	df	Survival		Above-ground biomass		Flowering		Flower number	
			LRT ^b	p	LRT ^b	p	LRT ^b	p	LRT ^b	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) ^c	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			SD	Levels	SD	Levels	SD	Levels	SD	Levels
Target species ^d			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				1,512		1,103		1,104		497

Notes. ^aOrder indicates the sequence in which fixed terms were removed from the model for LRTs. ^bSignificances of the fixed terms were tested using log-likelihood ratio tests (LRT) comparing models with and without the term of interest. ^cFor competition (no competition, competition with native, competition with naturalized species), we created two dummy variables to contrast no competition versus competition and native versus 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). ^dStandard deviations for individual target species random effects for the saturated model are found in Supporting Information Table S1.

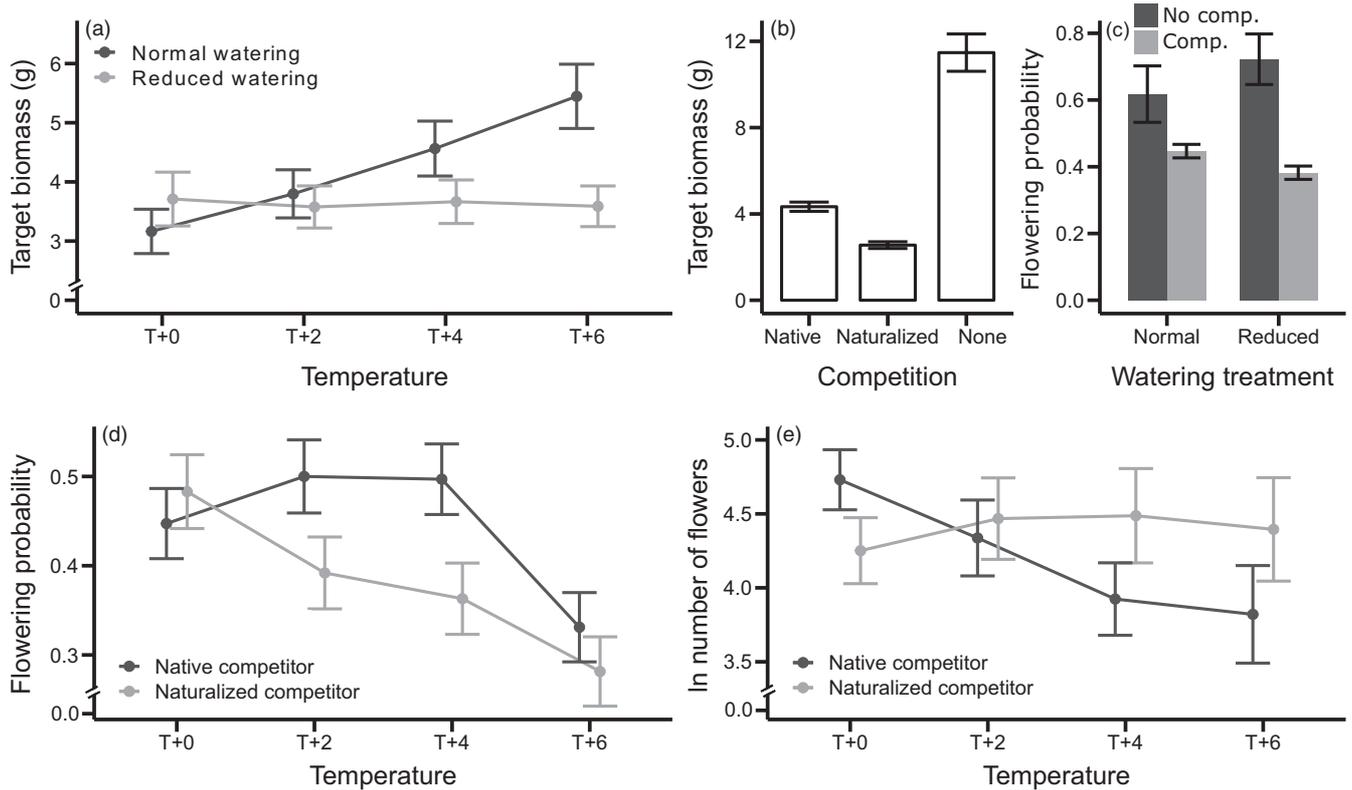


FIGURE 1 Target plant performance in terms of above-ground biomass (a, b), flowering (yes, no; c, d) and number of flowers (in the case of flowering, and natural-log transformed; e) in response to temperature (a, d, e) and watering (a, d) treatments, and across competition types (b–e). Error bars indicate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

TABLE 3 Results of generalized linear mixed-models (survival, flowering) and a linear mixed model (above-ground 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, that is proportion competitors surviving, total competitor above-ground biomass, and competitor flowering probability (yes, no). Significant ($p < 0.05$) effects are indicated in bold

Fixed effects	Order ^a	df	Survival		Above-ground biomass		Flowering	
			LRT ^b	<i>p</i>	LRT ^b	<i>p</i>	LRT ^b	<i>p</i>
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			SD	Levels	SD	Levels	SD	Levels
Target species ^c			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				1,431		1,436		1,427

Notes. ^aOrder indicates the sequence in which fixed terms were removed from the model for LRTs. ^bSignificances of the fixed terms were tested using log-likelihood ratio tests (LRT) comparing models with and without the term of interest. ^cStandard deviations for individual target species random effects for the saturated model are found in Supporting Information Table S1.

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

4 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 (Supporting Information Figure 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.

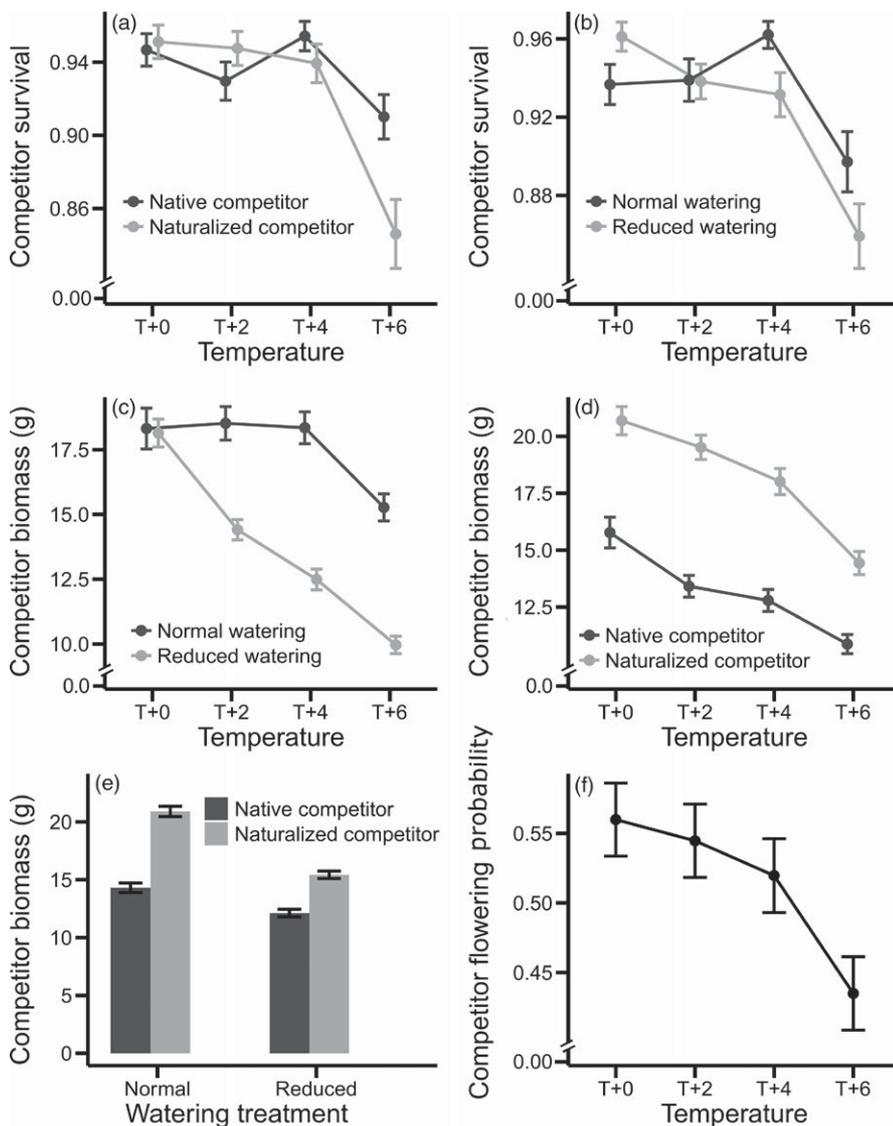


FIGURE 2 Competitor plant performance in terms of survival (proportion of plants surviving; a, b), above-ground biomass (c–e) and flowering probability of any competitor plants (yes, no; f) in response to temperature (a, b, c, d, f) and watering (b, c, e) treatments, for native and naturalized competitors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

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 above-ground biomass to total above-ground 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 Supporting Information Table S1

Fixed effects	Order	df	Target:total biomass ratio	
			LRT	<i>p</i>
Initial size	5	1	28.244	<0.0001
Climatic origin	4	1	3.666	0.056
Temperature	4	1	32.322	<0.0001
Watering	4	1	3.730	0.053
Competitor type	4	1	94.932	<0.0001
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			SD	Levels
Target species			<0.001	9
Competitor species			<0.001	20
Greenhouse			<0.001	4
Number observations				1,096

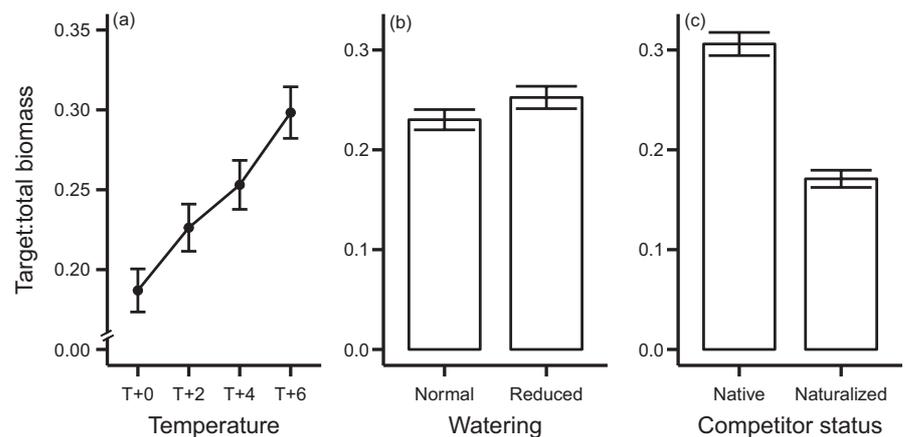


FIGURE 3 Ratio of target plant above-ground biomass to total above-ground biomass per pot across temperature treatments (a), under different watering regimes (b), and against native versus naturalized competitors (c). Error bars indicate standard errors

4.1 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 affected (Table 3, Figure 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

(Blumenthal, Chimner, Welker, & Morgan, 2007; Dukes & Mooney, 1999; 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 and 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-naturalized garden plants over resident species.

Above-ground biomass increased or was constant with increasing temperatures for non-naturalized species whereas it decreased for resident competitors. Consequently, the ratio of target to total above-ground 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 was lower 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 above-ground 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 below-ground tissues, which we could not measure, than the non-naturalized alien species, resulting in higher ratios of the target to total above-ground biomass per pot. Plants usually allocate more biomass to their roots when water availability is reduced (e.g., Fay, Carlisle, Knapp, Blair, & Collins, 2003; Quezada & Gianoli, 2010), and there is some evidence that naturalized alien plant species have higher shoot-mass fractions than native plants (e.g., Kuebbing, Classen, Sanders, & Simberloff, 2015; van Kleunen, Weber, & Fischer, 2010; Wilsey & Polley, 2006). 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 above-ground 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 (Figure 1c–e). However, those effects were weak compared to the negative response of competitor flowering to temperature increases (Figure 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-naturalized aliens over resident species will translate into higher reproductive output under climate change.

4.2 Responses and effects of differing resident competitor types

Naturalized competitors had more above-ground 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, Kaviani, & Tackenberg, 2014), selective introduction of more plastic genotypes (Bossdorf, Lipowsky, & Prati, 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 CO₂ 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., 2013), 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 and 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.

4.3 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.europealiens.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 (Supporting Information 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 (Supporting Information Figure 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, Blumenthal, Early, Grosholz, & Lawler, 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.

4.4 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 (IPCC, 2014; LUBW, 2013). 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, Dreesen, Janssens, and Nijs (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, Li, & Peng, 2012), or through the advancement of their phenology (Chuine et al., 2012). Other global-change components, such as increases in atmospheric CO₂ levels, will also likely interact with rising temperatures and changing precipitation to affect species to differing degrees (Alberto, Ziska, Cervancia, & Manalo, 1996; Farquhar, 1997; Long, 1991; Weltzin, Belote, & Sanders, 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 naturalization risk.

5 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 suggest 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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AUTHORS' CONTRIBUTIONS

E.H., M.v.K., and W.D. designed the study; E.H. implemented the study, collected the data, did the analyses with inputs from M.v.K. and W.D. and wrote the manuscript with the help of M.v.K. and W.D.

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REFERENCES

- Alberto, A. M. P., Ziska, L. H., Cervancia, C. R., & Manalo, P. A. (1996). The influence of increasing carbon dioxide and temperature on competitive interactions between a C₃ crop, rice (*Oryza sativa*) and a C₄ weed (*Echinochloa glabrescens*). *Functional Plant Biology*, *23*, 795–802.
- Altman, N., & Krzywinski, M. (2015). Split plot design. *Nature Methods*, *12*, 165–166.
- Anderson, N. O., Galatowitsch, S. M., & Gomez, N. (2006). Selection strategies to reduce invasive potential in introduced plants. *Euphytica*, *148*, 203–216.
- Bates, D., Machler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.
- Bellemare, J., & Deeg, G. (2015). Horticultural escape and naturalization of *Magnolia tripetala* in western Massachusetts: Biogeographic context and possible relationship to recent climate change. *Rhodora*, *117*, 71–83.
- Blumenthal, D., Chimner, R. A., Welker, J. M., & Morgan, J. A. (2007). Increased snow facilitates plant invasion in mixedgrass prairie. *New Phytologist*, *179*, 440–448.
- Bossdorf, O., Lipowsky, A., & Prati, D. (2008). Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Diversity and Distributions*, *14*, 676–685.
- Bradley, B. A., Blumenthal, D. M., Early, R., Grosholz, E. D., & Lawler, J. J. (2012). Global change, global trade, and the next wave of plant invasions. *Frontiers in Ecology and the Environment*, *10*, 20–28.
- Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution*, *25*, 310–318.
- Chrobock, T., Kempel, A., Fischer, M., & van Kleunen, M. (2011). Introduction bias: Cultivated alien plant species germinate faster and more abundantly than native species in Switzerland. *Basic and Applied Ecology*, *12*, 244–250.
- Chuine, I., Morin, X., Sonie, L., Collin, C., Fabreguettes, J., Degueldre, D., ... Roy, J. (2012). Climate change might increase the invasion potential of the alien C₄ grass *Setaria parviflora* (Poaceae) in the Mediterranean Basin. *Diversity and Distributions*, *18*, 661–672.
- Colgrave, N., & Ruxton, G. D. (2017). Using biological insight and pragmatism when thinking about pseudoreplication. *Trends in Ecology and Evolution*, *33*, 28–35.
- Cullen, J., Knees, S. G., Cubey, H. S., & Shaw, J. M. H. (Eds.) (2011). *The European garden flora flowering plants: A manual for the identification of plants cultivated in Europe, both out-of-doors and under glass*. Chicago, IL: The University of Chicago Press.
- de Boeck, H. J., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2011). Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. *New Phytologist*, *189*, 806–817.
- Dostál, P. (2011). Plant competitive interactions and invasiveness: Searching for the effects of phylogenetic relatedness and origin on competition intensity. *The American Naturalist*, *177*, 655–667.
- Dukes, J. S., & Mooney, H. A. (1999). Does global change increase the success of biological invaders? *Trends in Ecology and Evolution*, *14*, 135–139.
- Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gattlinger, A., ... Dullinger, S. (2017). Climate change will increase the naturalization risk from garden plants in Europe. *Global Ecology and Biogeography*, *26*, 43–53.
- Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hülber, K., Jarošík, V., ... Pyšek, P. (2011). Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 203–207.
- Farquhar, G. D. (1997). Carbon dioxide and vegetation. *Science*, *278*, 1411.
- Fay, P. A., Carlisle, J. D., Knapp, A. K., Blair, J. M., & Collins, S. L. (2003). Productivity responses to altered rainfall patterns in a C₄-dominated grassland. *Oecologia*, *137*, 245–251.
- Fay, P. A., & Schultz, M. J. (2009). Germination, survival, and growth of grass and forb seedlings: Effects of soil moisture variability. *Acta Oecologica*, *35*, 679–684.
- Feng, Y., Maurel, N., Wang, Z., Ning, L., Yu, F. H., van Kleunen, M., & Fleishman, E. (2016). Introduction history, climatic suitability, native range size, species traits and their interactions explain establishment of Chinese woody species in Europe. *Global Ecology and Biogeography*, *25*, 1356–1366.
- Frei, E. R., Ghazoul, J., Matter, P., Heggli, M., & Pluess, A. R. (2014). Plant population differentiation and climate change: Responses of grassland species along an elevational gradient. *Global Change Biology*, *20*, 441–455.
- Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist, G. W., & Holt, R. D. (2010). A framework for community interactions under climate change. *Trends in Ecology & Evolution*, *25*, 325–331.
- Grotkopp, E., & Rejmánek, M. (2007). High seedling relative growth rate and specific leaf area are traits of invasive species: Phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany*, *94*, 526–532.
- Haeuser, E., Dawson, W., & van Kleunen, M. (2017). The effects of climate warming and disturbance on the colonization potential of ornamental alien plant species. *Journal of Ecology*, *105*, 1698–1708.
- Haeuser, E., Dawson, W., & van Kleunen, M. (2018). Data from: Introduced garden plants are strong competitors of native and alien residents under simulated climate change. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.f5r163j>

- He, W. M., Li, J. J., & Peng, P. H. (2012). A congeneric comparison shows that experimental warming enhances the growth of invasive *Eupatorium adenophorum*. *PLoS ONE*, *7*, 3–7.
- Hulme, P. E. (2011). Addressing the threat to biodiversity from botanic gardens. *Trends in Ecology and Evolution*, *26*, 168–174.
- IPCC. (2014). Climate change 2014 synthesis report summary chapter for policymakers. In C. B. Field, V. R. Barros, D. J. Dokken & E. Al (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects*. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (pp. 1–190). Geneva, Switzerland: World Meteorological Organization.
- Kitajima, K., Fox, A. M., Sato, T., & Nagamatsu, D. (2006). Cultivar selection prior to introduction may increase invasiveness: Evidence from *Ardisia crenata*. *Biological Invasions*, *8*, 1471–1482.
- Kuebbing, S. E., Classen, A. T., Sanders, N. J., & Simberloff, D. (2015). Above- and below-ground effects of plant diversity depend on species origin: An experimental test with multiple invaders. *New Phytologist*, *208*, 727–735.
- Kuebbing, S. E., & Nuñez, M. A. (2016). Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. *Nature Plants*, *2*, 16134.
- Leiblein-Wild, M. C., Kaviani, R., & Tackenberg, O. (2014). Germination and seedling frost tolerance differ between the native and invasive range in common ragweed. *Oecologia*, *174*, 739–750.
- Liu, Y., Odour, A. M. O., Zhang, Z., Manea, A., Tooth, I. M., Leishman, M., ... van Kleunen, M. (2017). Do invasive alien plants benefit more from global environmental change than native plants? *Global Change Biology*, *23*, 3363–3370.
- Llorens, L., & Peñuelas, J. (2005). Experimental evidence of future drier and warmer conditions affecting flowering of two co-occurring mediterranean shrubs. *International Journal of Plant Sciences*, *166*, 235–245.
- Long, S. P. (1991). Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO₂ concentrations: Has its importance been underestimated? *Plant, Cell and Environment*, *14*, 729–739.
- LUBW (2013). *Zukünftige Klimaentwicklung in Baden-Württemberg - Perspektiven aus regionalen Klimamodellen*. Karlsruhe, Germany: LUBW.
- Manea, A., Sloane, D. R., & Leishman, M. R. (2016). Reductions in native grass biomass associated with drought facilitates the invasion of an exotic grass into a model grassland system. *Oecologia*, *181*, 175–183.
- Maurel, N., Hanspach, J., Kühn, I., Pysek, P., & van Kleunen, M. (2016). Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Global Ecology and Biogeography*, *25*, 1500–1509.
- Mayer, K., Haeuser, E., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... van Kleunen, M. (2017). Current and future local naturalization potential of ornamental species planted in urban green spaces and private gardens. *Biological Invasions*, *19*, 3613–3627.
- Moodley, D., Geerts, S., Richardson, D. M., & Wilson, J. R. U. (2013). Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. *PLoS ONE*, *8*, 1–8.
- NOAA. (2015). *Climate data online*. Retrieved from <https://www.ncdc.noaa.gov/data-access>
- Parepa, M., Fischer, M., & Bossdorf, O. (2013). Environmental variability promotes plant invasion. *Nature Communications*, *4*, 1604.
- Pattison, R. R., & Mack, R. (2008). Potential distribution of the invasive tree *Triadica sebifera* (Euphorbiaceae) in the United States: Evaluating CLIMEX predictions with field trials. *Global Change Biology*, *14*, 813–826.
- Pemberton, R. W., & Liu, H. (2009). Marketing time predicts naturalization of horticultural plants. *Ecology*, *90*, 69–80.
- Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D.; R Core Team. (2017). *nlme: Linear and nonlinear mixed effects models*. R package version 3.1-131. Retrieved from <https://CRAN.R-project.org/package=nlme>
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Kreft, H., ... van Kleunen, M. (2017). Naturalized alien flora of the world. *Preslia*, *89*, 203–274.
- Quezada, I. M., & Gianoli, I. (2010). Counteractive biomass allocation responses to drought and damage in the perennial herb *Convolvulus demissus*. *Austral Ecology*, *35*, 544–548.
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Richardson, D. M., Pyšek, P., Rejmánek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions*, *6*, 93–107.
- Sax, D. F., Early, R., & Bellemare, J. (2013). Niche syndromes, species extinction risks and management under climate change. *Trends in Ecology and Evolution*, *28*, 517–523.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*, 103–113.
- Schrama, M., & Bardgett, R. D. (2016). Grassland invasibility varies with drought effects on soil functioning. *Journal of Ecology*, *104*, 1250–1258.
- Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*, 21–32.
- Sorte, C. J. B., Ibáñez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., ... Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, *16*, 261–270.
- timeanddate.com. (2015). Konstanz, Baden-Württemberg, Germany – Sunrise, sunset. Retrieved from timeanddate.com
- Trusty, J. L., Lockaby, B. G., Zipperer, W. C., & Goertzen, L. R. (2008). Horticulture, hybrid cultivars and exotic plant invasion: A case study of *Wisteria* (Fabaceae). *Botanical Journal of the Linnean Society*, *158*, 593–601.
- Van der Veken, S., Hermy, M., Vellend, M., Knapen, A., & Verheyen, K. (2008). Garden plants get a head start on climate change. *Frontiers in Ecology and the Environment*, *6*, 212–216.
- van Kleunen, M., Dawson, W., Bossdorf, O., & Fischer, M. (2014). The more the merrier: Multi-species experiments in ecology. *Basic and Applied Ecology*, *15*, 1–9.
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103.
- van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., ... Dehnen-Schmutz, K. (2018). The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews*, *93*, 1421–1437. <https://doi.org/10.1111/brv.12402>
- van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*, 235–245.
- Walther, G. R., Gritti, E. S., Berger, S., Hickler, T., Tang, Z., & Sykes, M. T. (2007). Palms tracking climate change. *Global Ecology and Biogeography*, *16*, 801–809.
- Weltzin, J. F., Belote, R. T., & Sanders, N. J. (2003). Biological invaders in a greenhouse world: Will elevated CO₂ fuel plant invasions? *Frontiers in Ecology and the Environment*, *1*, 146–153.
- Williams, A. L., Wills, K. E., Janes, J. K., Vander Schoor, J. K., Newton, P. C. D., Hovenden, M. J., & Hovenden, M. (2007). Warming and free-air CO₂ enrichment alter demographics in four co-occurring grassland species. *New Phytologist*, *176*, 365–374.
- Willis, C. G., Ruhfel, B. R., Primack, R. B., Miller-rushing, A. J., Jonathan, B., & Davis, C. C. (2010). Favorable climate change response explains non-native species' success in Thoreau's woods. *PLoS ONE*, *5*, e8878.

- Wilsey, B. J., & Polley, H. W. (2006). Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia*, 150, 300–309.
- Wittenburg, R., & Cock, M. J. W. (2005). Best practices for the prevention and management of invasive alien species. In H. A. Mooney, R. N. Mack, J. A. McNeely, L. E. Neville, P. J. Schei, & J. K. Waage (Eds.), *Invasive alien species: A new synthesis* (pp. 209–232). Washington, DC: Island Press.
- World Weather Online. 2016. Worldweatheronline.com. Retrieved from <http://www.worldweatheronline.com>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. In M. Gail, K. Krickeberg, J. M. Samet, A. Tsiatis, & W. Wong (Eds.). New York, NY: Springer Science and Business Media.