The context-depency of biological invasions makes it difficult to understand why some species become successful invaders and others not. Such understanding requires studying closely-related invasive and non-invasive alien taxa sharing the same introduction history in the same environment. We identified this unusual situation in Kenya where the individuals that founded invasive *Prosopis juliflora* and non-invasive *P. pallida* populations are still present in original plantations. We evaluated field-measured traits, conducted glasshouse experiments simulating different nitrogen and water availability treatments, and did reciprocal transplants to compare functional traits and plasticity between the founders of both species (i.e. ‘invasive–non-invasive congeners’ comparison), and between *P. juliflora* individuals from plantations and invaded sites (i.e. testing for rapid evolution during invasion). We found that planted individuals of *P. juliflora* and *P. pallida* differed in a number of key traits related to performance and spread (root:shoot ratio, number of stems and susceptibility to seed damage) as well as in levels of phenotypic plasticity in growth responses to resource availability, which may explain their differential invasiveness. Offspring of invasive *P. juliflora* individuals had higher seed mass and production, germination, survival, produced more stems, matured earlier and had higher plasticity compared with those of founder individuals, indicative of rapid post-introduction evolution. By using this exceptional study system, we show that differences in values of only a few key traits, increased phenotypic plasticity and post-introduction evolution have all contributed to the success of *P. juliflora* as an invasive species in Kenya.

Keywords: common garden, environmental stress, invasiveness, phenotypic plasticity, rapid evolution, tree invasions, woody invasive species
Introduction

Several studies have addressed whether particular traits can be linked to the likelihood of a species becoming invasive (Rejmanek and Richardson 1996, Goodwin et al. 1999, Pyšek and Richardson 2007). This research effort has resulted in many ecological and evolutionary hypotheses to explain invasion success (Catford et al. 2009, Enders et al. 2018, 2020) and to identify generalities that could aid risk assessments and management efforts (Novoa et al. 2020). However, the context-dependence of biological invasions makes it difficult to understand why some species become successful invaders and others not (Catford et al. 2019). For such understanding it is necessary to perform comparative studies on organisms with different levels of invasiveness (van Kleunen et al. 2010a) sharing the same introduction history, residence times (Wilson et al. 2007) and propagule pressure (Colautti et al. 2006), in the same environment. However, these circumstances are rare anywhere on Earth.

From an ecological viewpoint, many invasion hypotheses are formulated around functional traits, including those related to dispersal, growth responses and reproduction (Catford et al. 2009, Enders et al. 2018, 2020). Invasiveness has also been attributed to the release from natural enemies in the invaded areas (i.e. enemy release hypothesis; Keane and Crawley 2002, Heger and Jeschke 2018). Differential species invasiveness may also be associated with differences in phenotypic plasticity of traits – broadly defined as the capability of one genotype to display different phenotypes in response to different environmental conditions, and thus increasing survival and reproduction (Richards et al. 2006, Davidson et al. 2011, Liao et al. 2016).

The evolutionary school of thought suggests that non-native species often undergo rapid evolution to become invasive (Bosdorf et al. 2005, Maron et al. 2007, Moran and Alexander 2014, van Kleunen et al. 2018). Such evolution can occur through deterministic processes, e.g. in response to novel selection pressures such as herbivory, mutualistic interactions and altered abiotic conditions (Barrett et al. 2008, Pretis et al. 2008, Moran and Alexander 2014, Zenni et al. 2014, Reznick et al. 2019). In contrast, non-adaptive shifts in genotype and phenotype frequencies in invasive populations may stem from demographic events during range expansion such as strong founder events, genetic drift or spatial sorting (Shine et al. 2011, Perkins et al. 2013, Schriever et al. 2017, Clarke et al. 2019). Studies searching for evidence of rapid post-introduction evolution often use the analogy of ‘ancestor–descendant’ comparisons, by studying the genetic basis of phenotypic variation within and among populations from the native and the invaded range (Rogers and Siemann 2004, Keller and Taylor 2008, Stutz et al. 2018). However, such studies rarely involve the actual ‘ancestors’ of invasive lineages. This is because the original founders of invasive populations are either dead or cannot be located; the native geographic origins of the introduced populations are unknown; invasive populations may comprise genetic admixtures between different native sources; or invasive populations are severely bottle-necked (Keller and Taylor 2008, Colautti and Lau 2015).

Some of the world’s worst invasive trees belong to the genus *Prosopis* (Leguminosae). *Prosopis* species have been introduced to more than 129 countries and have become naturalized or invasive in 122 of these, having negative effects on ecosystems, economy and society (Shackleton et al. 2014). *Prosopis* introductions in eastern Africa provide a truly unique opportunity to study differences in invasiveness between species and the eco-evolutionary processes that underlie successful invasion. In Baringo County, Kenya, plantations of two species, *Prosopis juliflora* and *P. pallida*, that were established in the early 1980s (Johansson 1990, Otsamo and Maua 1993, Choge et al. 2002), are still present today at known locations (Choge et al. 2002, Mbaabu et al. 2019). Thus, they share similar residence times under similar ecological conditions. Introductions of *Prosopis* individuals also involved seeds from a few individuals of each species (Choge et al. 2002). Large-scale invasion of landscapes surrounding these plantations by *P. juliflora* has been documented multiple times (Choge et al. 2002, Castillo 2019, Mbaabu et al. 2019), while *P. pallida* individuals have only occasionally been detected outside plantations (Castillo 2019). Here, we aim to investigate why one species (*P. juliflora*) has become invasive while the other (*P. pallida*) has not, and whether rapid post-introduction evolution occurred during invasion by *P. juliflora*. To do this we compared functional traits and their plasticity of a) the offspring of trees of both species that were originally planted and b) the offspring of planted *P. juliflora* trees, and trees that have invaded areas outside plantations. The first comparison could provide insight into the determinants of invasiveness at the species level, while the second comparison would be, to our knowledge, one of the first to compare the founders of a species with their invasive descendants to assess evidence for rapid evolution during invasion.

Specifically, we tested two hypotheses: 1) that planted (i.e. founder) *P. juliflora* differs from planted *P. pallida* in functional traits, their plasticity and allometric growth allocation, supportive of differences in their invasiveness; and 2) that invasive individuals of *P. juliflora* differ from planted *P. juliflora* individuals in functional traits, their plasticity and allometric growth allocation, supportive of rapid evolution during invasion. To this end, we evaluated field-measured traits related with reproductive output of planted *P. juliflora* and *P. pallida* trees and invasive *P. juliflora* individuals, and conducted glasshouse and reciprocal transplant experiments to compare traits associated with invasiveness, involving offspring from founder trees as well as offspring from invasive *P. juliflora* trees.

Material and methods

Study area and study species

Our study area was located in Baringo County, Kenya, which is ca 50 km north of the equator. The climate is semi-arid (Owen et al. 2004) with a yearly average temperature of 24.6°C (Kassilly 2002). The area has two wet seasons, and the mean annual rainfall is 635 mm (Kassilly 2002).
Prosopis juliflora and P. pallida share similar environmental tolerances and morphological characteristics, with some authors considering them a species complex (Pasiecznik et al. 2001). In some non-native ranges, both species are considered highly invasive and as ecosystem transformers (Pasiecznik et al. 2001, Shackleton et al. 2014). It is thought that the global invasion success of Prosopis species is linked to their high performance under conditions of low soil nitrogen and water availability (Geesing et al. 2000, Pasiecznik et al. 2001, Shackleton et al. 2014). For example, in Ethiopia P. juliflora invades large areas with nutrient-poor and dry soils (MLC pers. obs.) where it negatively impacts biodiversity and ecosystem services (Linders et al. 2019, 2021). Further details of our study area and both species are provided in the Supporting information.

Seed collection

For common garden experiments, we collected seeds from 55 healthy and mature and haphazardly selected trees, representing both planted (n = 28) and invasive (n = 27) trees from randomly selected sites. Planted trees were from seven plantations, and with either one or both of the Prosopis species present. Invasive trees were from nine sites, all of them having mature trees and seedlings, indicating ongoing reproduction and spread. Details on morphological classification of study species are provided in the Supporting information. Hereafter ‘origin’ refers to either plantation or invaded areas while ‘origin site’ refers to each one of the seven plantation sites or nine invaded sites. Each mature tree was characterized according to its origin and species type, i.e. as being either invasive P. juliflora, plantation P. juliflora or plantation P. pallida (Supporting information). We did not observe any P. pallida trees in invaded areas and genetic analyses confirmed that only P. juliflora is invasive in the area (Castillo 2019, Castillo et al. 2021).

From these trees, between five and 30 seed pods were collected per individual. Differences in the number of seeds collected per tree were due to high variation in seed set and seed damage between individuals within and between sites. From subsets of the trees, we also determined the number of seeds per pod (n = 51 individuals), the percentage of undamaged seeds per pod (n = 51 individuals), and the seed mass per pod (n = 50 individuals). Although 55 trees were sampled, only 54 had enough replicates to be used in the experiments (Table 1 for methodology for data collection of traits).

Comparison of reproductive output between planted Prosopis juliflora and P. pallida

We fitted linear mixed-effect models (LMMs) using the nlme R package (Pinheiro et al. 2017) for seed mass, number of seeds (both log-transformed to satisfy model assumptions) and percentage of undamaged seeds, including the tree species as fixed effects. Origin site was set as random effect to account for spatio–temporal autocorrelation. To account for maternal effects on number of seeds and percentage of undamaged seeds, parent trees was added as random effect, nested in origin site.

Comparison of reproductive output between invasive and planted P. juliflora individuals

We fitted LMMs as above (i.e. same random factor terms for each response variables), for the same response variables, but including the origin of P. juliflora as fixed factor (i.e. invasive or planted).

Table 1. Summary of models fitted for different trait data from the reciprocal transplant experiment. The first set of models comparing the two Prosopis species included transplant site and tree species (plantation P. juliflora and plantation P. pallida) as fixed factors, while the second set of models comparing planted and invasive P. juliflora included transplant site (invaded and plantation) and origin of P. juliflora (i.e. invasive versus plantation) as fixed factors. A random factor was included in models with height and stem diameter as response variables. This random factor was not included in models with the number of stems as response variable as it caused model overfitting (see Material and methods for model details and transformation of variables).

| Trait               | N_ind | Transplant site | Tree species | Interaction | Random effects |
|---------------------|-------|-----------------|--------------|-------------|----------------|
|                     |       | F – χ² (df) p   | F – χ² (df) p| F – χ² (df) p| Plantation-invaded site pair/origin site/parent tree |
| Height              | 167   | 16.11 (1,147) < 0.001 | 5.04 (1,14) < 0.05 | 0.88 (1,147) 0.35 | 0.10            |
| Stem diameter       | 167   | 3.17 (1,147) 0.08  | 8.33 (1,14) < 0.05 | 0.98 (1,147) 0.32 | 0.14 |
| Number of stems     | 167   | 0.25 (1) 0.62    | 14.30 (1) < 0.001 | 0.53 0.47          | –               |

| Trait               | N_ind | Transplant site | Origin P. juliflora | Interaction | Random effects |
|---------------------|-------|-----------------|---------------------|-------------|----------------|
|                     |       | F – χ² (df) p   | F – χ² (df) p       | F – χ² (df) p| Plantation-invaded site pair/origin site/parent tree |
| Height              | 317   | 44.97 (1,289) < 0.001 | 0.38 (1,4) 0.57  | <0.01 0.97 | <0.01            |
| Stem diameter       | 317   | 8.58 (1,289) < 0.01 | 0.65 (1,4) 0.47 | 0.23 (1,289) 0.63 | 0.09 |
| Number of stems     | 317   | 0.18 (1) 0.67    | 4.35 (1) < 0.05 | 0.05 (1) 0.82 | –               |

N_ind = total number of individuals. df = degrees of freedom. Bold p-values indicate significance levels < 0.05.
Reciprocal transplant experiment

To evaluate the determinants of invasiveness at species level and to test for rapid evolution during *P. juliflora* invasion, we conducted a reciprocal transplant experiment involving offspring from planted trees of both *Prosopis* species and offspring from invasive *P. juliflora* trees. We then compared traits related to invasiveness between the planted tree species (i.e. ‘invasive–non-invasive congener’ comparison) and between planted and invasive *P. juliflora* trees (i.e. ‘ancestor–descendant’ comparisons). The experiment was conducted using a subset of our sampled sites: three plantation sites where both *P. juliflora* and *P. pallida* were originally planted (and are still present), and five invaded sites (Supporting information). We paired 1–2 invaded sites randomly to a plantation site as there is 1) weak genetic structure between founder and invasive *P. juliflora* populations, 2) no genetic structure between invasive *P. juliflora* populations (Castillo 2019), 3) no significant difference between invaded and plantation sites in soil chemistry, nor soil textures, 4) no spatial correlation between sites for soil characteristics and the landscape variables that influence the distribution of *Prosopis* in Baringo (e.g. elevation, precipitation in the wettest month, Eckert et al. 2020; Fig. 1, Supporting information).

In July of 2016 seeds from the selected plantation and invaded sites were germinated. Five seeds from the same tree (i.e. same maternal line) were sown in the same pot containing soil from their origin site in a common garden. *Prosopis* seedlings were randomly weeded after emergence, leaving only one seedling per pot. Seedlings were transplanted in the field between 14 and 21 November 2016 (details of the experimental design are provided in the Supporting information). For each plantation/invaded site group, transplants only involved seedlings from that specific combination (Fig. 1, Supporting information). The number of maternal lines replicated in each plantation and invaded site is provided in the Supporting information. Around 150 individuals for each plantation-invaded site pair were included (total of 447 individuals for the three pairs).

At 15 months after transplanting individuals in the field, we recorded stem diameter, height and the number of stems for each individual. Traits related with reproduction such as any sign of flowering, age at maturity and number of inflorescences and pods per individual were also recorded 17 months post-germination.

Comparisons of planted *Prosopis juliflora* and *P. pallida*

We fitted models with transplant site (plantation or invaded) and the tree species as fixed effects for height, stem diameter (log-transformed) and number of stems. LMMs were fitted for height and stem diameter with parent tree nested in origin site which was nested in plantation-invaded site pair as random factor. For number of stems, random factors indicated above caused overfitting of the model, therefore, we used generalised linear models (GLMs) with Poisson distributions and logit link functions.

We report on model results using parent trees instead of seed mass as a random effect because the effect of seed mass did not change the significance of any of the fixed terms and/or interaction terms and seedlings from parent trees without this data had to be removed from the analyses. For comparison, results of the effect of both parent tree and seed mass are shown in Table 2 and Supporting information. Since only fixed effects were of biological importance for assessing the factors that contribute to invasiveness, we pay particular attention to these in the ‘Results’ section. See also the Supporting information for testing of the significance of fixed factors and their interactions.

Comparisons of invasive and planted *P. juliflora* individuals

We fitted models as above (i.e. using the same random factors), with the same response variables, but including transplant site and the origin of *P. juliflora* as fixed factors. A significant interaction term between fixed factors would indicate local adaptation (Kawecki and Elbert 2004). In the absence of a significant interaction, a significant origin effect would still provide evidence for rapid evolution between plantation and invasive *P. juliflora* individuals. For comparison, results of the effect of both parent tree and seed mass are shown in Table 2 and Supporting information. See Supporting information for testing of the significance of fixed factors and their interactions.

Glasshouse experiment

We also performed a glasshouse experiment to compare the means of key performance traits, phenotypic plasticity of growth traits and biomass allocation strategies, between planted (founder) *Prosopis* tree species to test for differences of invasiveness at inter-specific level; and between planted and invasive *P. juliflora* trees to test for rapid evolution during invasion of this species. The experiment was conducted at Stellenbosch University, South Africa, between June and November 2017, using seeds from parent trees originating from seven plantation and seven invaded sites. The number of parent trees used for seed collections of planted *P. juliflora* and *P. pallida* and invasive *P. juliflora*, is provided in the Supporting information. Five seeds from the same maternal line were sown in 30 cm-deep pots filled with a 2:3 silica sand–vermiculite mixture. A total of 350 pots were included in the experiment. The percentage of germination and mean emergence time (MET) were recorded for each individual pot. Seedlings were randomly weeded out 15–20 days after emergence, leaving only one seedling per pot. At this time seedling survival for each individual pot was recorded. After four weeks of growth, pots were selected at random for each treatment and rotated weekly until harvesting. For each treatment, a mean of 18.5 replicates (i.e. number of individual pots/treatment) for plantation *P. pallida*, 20 replicates for plantation *P. juliflora* and 30.5 replicates for invasive *P. juliflora* were included; leading to a total of 276 individual treatment combinations (total number of replicates was reduced due to germination failure or no survival of seedlings in some pots). The number of maternal lines replicated in each treatment is shown in the Supporting information. The following
treatments were applied in a full factorial design: water (low and high availability) and nitrogen (low and high availability), the details of which are provided in the Supporting information.

After 20 weeks of growth, eight traits were measured for each seedling: root and stem length, biomass of roots, leaves and shoots, root to shoot ratio (RSR), number of leaves and total plant biomass (see the Supporting information for methodology).

**Comparisons of planted Prosopis juliflora and P. pallida**

We fitted models with tree species as fixed factor for percentage of germination, MET and survival. The latter was estimated at the time of weeding the pots and therefore it was not affected by the water and nitrogen treatment. General mixed-effect models (GLMMs) were fitted for percentage of germination and survival, with parent tree as random factor using the *lme4* R package (Bates et al. 2017). For MET, we used GLM since the model was overfitted with parent tree as random factor.

LMMs were fitted for root length, stem length, root biomass, stem biomass, RSR, leave biomass and total plant biomass (all log-transformed). For number of leaves we fitted GLMMs. These models were fitted with tree species, nitrogen treatment, water treatment and their interactions as fixed factors. Parent tree nested in origin site was considered as random variable, except for number of leaves, were only parent tree was added as random factor due to overfitting of the model.

MET was not added as covariable in the models because it did not have a significant effect on survival ($\chi^2 = 0.12; p = 0.73$). Similarly, as per reciprocal transplant experiment,
Table 2. Summary of mixed-effect models fitted for different trait data from the glasshouse experiment. A first model had water treatment (high/low), nitrogen treatment (high/low), tree species (plantation *P. juliflora* and plantation *P. pallida*) and their interactions as fixed factors. The second model was fitted using water treatment, nitrogen treatment, origin of *P. juliflora* (invasive *P. juliflora* and plantation *P. juliflora*) and their interactions (see Material and methods for model details and transformation of variables), as fixed factors. Bold p-values indicate significance levels < 0.05.

| Response variable | Tree species | Interaction tree species – water | Interaction tree species – Nitrogen | Interaction water – Nitrogen | Interaction all | Origin site / parent tree | SD explained |
|-------------------|--------------|---------------------------------|-----------------------------------|-----------------------------|---------------|--------------------------|-------------|
| Trait             | N_{ind}      | F – χ² (df) p                  | F – χ² (df) p                     | F – χ² (df) p               | F – χ² (df) p | F – χ² (df) p            |             |
| Root length       | 125          | 1.79 (1,11) 0.21                | 8.61 (1,100) < 0.01               | 4.11 (1,100) 0.05           | 1.89 (1,100) 0.17 | 0.15 (1,100) 0.70 | <0.01       |
| Stem length       | 136          | 47.63 (1,11) < 0.001            | 5.63 (1,111) < 0.05               | 1.23 (1,111) 0.27           | 6.84 (1,111) < 0.05 | 1.84 (1,111) 0.18 | 0.02        |
| Root biomass      | 66           | 2.66 (1,11) 0.14                | 2.96 (1,41) 0.09                  | 0.02 (1,41) 0.90            | 3.11 (1,41) 0.08 | 0.20 (1,41) 0.66 | 0.12        |
| Stem biomass      | 136          | 0.22 (1,11) 0.65                | 7.09 (1,111) < 0.05               | 0.74 (1,111) 0.39           | 17.46 (1,111) < 0.001 | 0.44 (1,111) 0.51 | 0.19        |
| RSR               | 66           | 13.57 (1,11) < 0.01             | 0.04 (1,141) 0.84                 | 1.69 (1,141) 0.20           | 0.68 (1,141) 0.42 | 0.59 (1,141) 0.45 | <0.01       |
| Leave biomass     | 139          | 0.97 (1,11) 0.35                | 3.17 (1,114) 0.08                 | 0.02 (1,114) 0.88           | 17.01 (1,114) < 0.001 | 1.71 (1,114) 0.19 | 0.17        |
| Number of leaves  | 131          | 0.22 (1) 0.64                   | 11.04 (1) < 0.001                 | 2.74 (1) 0.10               | 3.70 (1) 0.06 | 0.04 (1) 0.84 | 0.09†       |
| Total plant biomass | 66      | 1.43 (1,11) 0.26                | 2.95 (1,41) 0.09                  | 0.24 (1,41) 0.63           | 6.65 (1,41) < 0.05 | 0.10 (1,41) 0.76 | 0.17        |

| Trait             | N_{ind}      | Origin *P. juliflora* | Interaction origin *P. juliflora* – water | Interaction origin *P. juliflora* – Nitrogen | Interaction water – Nitrogen | Interaction all | Origin site / parent tree | SD explained |
|-------------------|--------------|-----------------------|--------------------------------------------|---------------------------------------------|-----------------------------|---------------|--------------------------|-------------|
| Root length       | 168          | 0.04 (1,9) 0.86       | 6.20 (1,136) < 0.05                        | 3.22 (1,136) 0.64                         | 0.52 (1,136) 0.47           | 5.76 (1,136) < 0.05 | 0.02        |
| Stem length       | 176          | 2.37 (1,9) 0.16       | 8.88 (1,144) < 0.01                        | 9.32 (1,144) < 0.01                       | 37.03 (1,144) < 0.001       | 5.69 (1,144) < 0.05 | 0.26        |
| Root biomass      | 94           | 0.30 (1,9) 0.60       | 1.14 (1,62) 0.29                            | 0.71 (1,62) 0.40                          | 13.97 (1,62) 0.43           | 0.63 (1,62) 0.43 | 0.10        |
| Stem biomass      | 179          | 1.68 (1,9) 0.23       | 10.46 (1,147) < 0.01                        | 0.08 (1,147) 0.78                         | 32.70 (1,148) < 0.001       | 0.20 (1,147) 0.66 | 0.16        |
| RSR               | 89           | 0.77 (1,9) 0.40       | 0.89 (1,57) 0.35                            | 0.16 (1,57) 0.69                          | 3.74 (1,57) 0.06             | 0.62 (1,57) 0.44 | 0.15        |
| Leaf biomass      | 183          | 0.08 (1,9) 0.78       | 12.21 (1,151) < 0.001                       | 2.13 (1,151) 0.15                         | 40.87 (1,151) < 0.001       | 0.09 (1,75) 0.75 | 0.15        |
| Number of leaves  | 174          | 0.01 (1) 0.93         | 16.60 (1) < 0.001                           | 1.07 (1) 0.30                             | 6.00 (1) < 0.05             | <0.01 (1) 0.97 | 0.06†       |
| Total plant biomass | 90      | 0.80 (1,9) 0.39       | 2.61 (1,58) 0.11                            | 1.72 (1,58) 0.20                          | 14.27 (1,58) < 0.001        | 0.54 (1,58) 0.46 | 0.06        |

N_{ind} = total number of individuals; RSR = root:shoot ratio; df = degrees of freedom.

In all models the fixed factors, water and nitrogen treatment, had significant effects on response variables (p < 0.05; F – χ² tests).

† Random factor term had only parent tree due to model overfitting.
we tested seed mass as a random term instead of parent tree, but the effect of seed mass did not change the significance of any of the fixed and/or interaction terms. Therefore, results are based on models using parent tree instead seed mass as a random effect. See the Supporting information for results of the effect of seed mass as random factor. The distribution and link function used in models and methods for testing of the significance of all fixed factors and their interactions in all models are given in the Supporting information.

We also estimated the phenotypic plasticity of growth traits by determining the coefficient of variation as the standard deviation of trait means/mean of trait means (Schlichting and Levin 1986, Valladares et al. 2002, 2006). We then calculated differences between planted tree species in: 1) plasticity for each trait, 2) the mean plasticity for nitrogen and water availability independently and 3) in the mean plasticity across nitrogen and water treatments.

Lastly, we estimated differences in allometric biomass allocation, i.e. the degree of investment in a given trait per unit biomass produced, across treatments for each growth trait as the relationship between Ln(total plant biomass) and each Ln-transformed trait measure, using standardized major axis (SMA) regression (Sokal and Rohlf 1995) that includes the variability of both variables. SMA slopes (i.e. ratio between traits) were tested for significant differences between tree species under different nitrogen and water availability conditions. From an allometric viewpoint, different slopes or different elevations suggest that growth allocation is affected by the treatments, indicating differences in static allometric slope for that particular trait. SMA regressions and tests were implemented using the SMATR package in R (Warton and Ormerod 2007).

Comparisons of invasive and planted \textit{P. juliflora} individuals

We fitted models as above, for percentage of germination and survival, but including transplant site and the origin of \textit{P. juliflora} as fixed factors. For the eight growth traits, we fitted the same models as per tree species comparison (all log-transformed except stem length) but with the origin of \textit{P. juliflora} as fixed factors. MET did not have a significant effect on survival ($\chi^2 = 3.07; p = 0.07$), so it was was not included as covariable in models. For comparison, results of the effect of both parent tree and seed mass are shown in Table 3 and the Supporting information. See also the Supporting information for distributions and link functions used in models for testing significance of all fixed factors and their interactions.

As per planted \textit{P. juliflora} and \textit{P. pallida} comparisons, but between \textit{P. juliflora} origins, we calculated differences in plasticity for: 1) each growth trait, 2) water and nitrogen treatments and 3) across treatments; and compared allometric biomass allocation of growth traits across treatments. We performed all analyses using R statistical language (www.r-project.org).

Results

Comparison of reproductive output between planted \textit{Prosopis juliflora} and \textit{P. pallida}

Both species produced similar numbers of seeds ($F_{1,20} = 3.54$, $p = 0.08$, Fig. 2a), of similar size ($F_{1,20} = 0.01$, $p = 0.91$, Fig. 2c), but susceptibility to seed damage was 37% lower in \textit{P. juliflora} ($F_{1,20} = 15.86, p < 0.001$, Fig. 2b).

Table 3. Plasticity indices (for invasive \textit{P. juliflora}, plantation \textit{P. juliflora} and plantation \textit{P. pallida}) under water and nitrogen treatments. Differences in plasticity were also estimated between tree species (plantation \textit{P. juliflora}–plantation \textit{P. pallida}) and between origin of \textit{P. juliflora} (invasive \textit{P. juliflora}–plantation \textit{P. juliflora}).

| Treatment | Trait    | Plasticity index | Difference in plasticity index |
|-----------|----------|-----------------|-------------------------------|
|           |          | Invasive \textit{P. juliflora} | Plantation \textit{P. juliflora} | Plantation \textit{P. pallida} | Between tree species | Between \textit{P. juliflora} origins |
| Water     | Root length | 0.12 | 0.01 | 0.16 | −0.16 | 0.11 |
|           | Stem length | 0.5  | 0.28 | 0.41 | 0.01  | 0.22 |
|           | Root biomass | 0.6  | 0.39 | 0.38 | 0.01  | 0.21 |
|           | Stem biomass | 0.89 | 0.55 | 0.76 | −0.21 | 0.34 |
|           | RSR      | 0.49 | 0.18 | 0.20 | −0.02 | 0.31 |
|           | Leaf biomass | 0.88 | 0.53 | 0.63 | −0.10 | 0.35 |
|           | Number of leaves | 0.45 | 0.21 | 0.34 | −0.13 | 0.24 |
|           | Total plant biomass | 0.71 | 0.49 | 0.46 | 0.03  | 0.22 |
|           | Treatment mean | 0.58 | 0.33 | 0.42 | −0.09 | 0.25 |
| Nitrogen  | Root length | 0.05 | 0.05 | 0.08 | −0.03 | 0.00 |
|           | Stem length | 0.45 | 0.24 | 0.3  | −0.06 | 0.21 |
|           | Root biomass | 0.55 | 0.39 | 0.24 | 0.15  | 0.16 |
|           | Stem biomass | 0.75 | 0.66 | 0.69 | −0.03 | 0.09 |
|           | RSR      | 0.42 | 0.2  | 0.27 | −0.07 | 0.22 |
|           | Leaf biomass | 0.78 | 0.56 | 0.52 | 0.04  | 0.22 |
|           | Number of leaves | 0.34 | 0.26 | 0.28 | −0.01 | 0.08 |
|           | Total plant biomass | 0.67 | 0.46 | 0.35 | 0.11  | 0.21 |
|           | Treatment mean | 0.50 | 0.35 | 0.34 | 0.01  | 0.15 |
Comparison of reproductive output between invasive and planted *P. juliflora* individuals

*Prosopis juliflora* from plantations produced 22% less seeds per pod than invasive individuals ($F_{1,10}=10.51$, $p<0.01$, Fig. 2a) and their seeds were 16% smaller ($F_{1,10}=6.77$, $p<0.05$, Fig. 2c). Levels of seed damage between origins were similar ($F_{1,10}=0.03$, $p=0.86$, Fig. 2b).

Reciprocal transplant experiment

Comparisons between *Prosopis juliflora* and *P. pallida*

Seedlings of both species grew taller in plantation sites than seedlings in invaded sites (Fig. 3a). Independently of sites, plantation *P. pallida* seedlings were, on average, 9% taller (Table 1, Fig. 3a), but had 33% narrower stem diameters (Table 1, Fig. 3b) and produced 34% less stems (Table 1, Fig. 3c), than plantation *P. juliflora* seedlings.

Comparisons of invasive and planted *P. juliflora* individuals

There was no origin × transplant site interactions for stem diameter, height and number of stems. *Prosopis juliflora* seedlings growing in plantations were taller (Table 1, Fig. 3a) and had larger stem diameters (Table 1, Fig. 3b) than those growing in invaded sites, and invasive individuals had, on average, 14% more stems than planted individuals (Table 1, Fig. 3c). At the time of the data collection (17 months post-germination), seven invasive *P. juliflora* seedlings had reached reproductive maturity (first production of flowers and/or presence of pods) while plantation *P. juliflora* did not show any signs of reproduction. These seven invasive *P. juliflora* individuals had between two and nine flowers and between one and 17 seed pods.

Glasshouse experiment

Comparisons between *Prosopis juliflora* and *P. pallida*

Germination percentages were similar for seeds of both species ($\chi^2 = 0.21$, $p=0.64$, Fig. 4a), but seeds of *P. juliflora* germinated 1.2 weeks later ($\chi^2 = 17.34$, $p<0.001$, Fig. 4b). Survival of plantation *P. pallida* and plantation *P. juliflora* seedlings did not differ ($\chi^2 = 0.67$, $p=0.41$, Fig. 4c). *Prosopis pallida* seedlings had 36% longer stems and 21% lower RSR than plantation *P. juliflora* seedlings, independent of the treatments (Table 2, Fig. 5b and e, respectively). Under high water availability, plantation *P. pallida* had 15% longer roots (Tukey HSD: $p<0.001$). Under low nitrogen availability plantation *P. pallida* tended to have longer roots than plantation *P. juliflora* (Tukey HSD: $p=0.05$, Table 2, Fig. 5a), and this difference remained significant when including seed mass as random factor instead of parent tree (Tukey HSD: $p<0.05$, Supporting information).

Overall, plantation *P. juliflora* showed different plasticity in various traits compared to plantation *P. pallida* (Table 3, Fig. 6). Across plant sizes, plantation *P. pallida* had proportionally longer stems and allocated more biomass to them than plantation *P. juliflora*, while the allocation of biomass to

Figure 2. Differences in reproductive output of parent trees of invasive *P. juliflora* (red), plantation *P. juliflora* (blue) and plantation *P. pallida* (green) depicted as (a) average number of seeds per pod, (b) the percentage of undamaged seeds per pod (i.e. seeds not aborted or showing signs of herbivore damage or fungal infection), (c) average seed mass per pod. These seeds were used in the common garden experiment. Separate models were used: one between tree species (i.e. plantation *P. juliflora* and plantation *P. pallida*) and a second between *P. juliflora* origins (i.e. invasive *P. juliflora* and plantation *P. juliflora*). Bars represent mean ± standard error. Statistical significance: *, $p<0.05$; **, $p<0.01$; ***, $p<0.001$ ($p<0.05$; $F$ – tests).
roots and leaves was proportionally similar between the two species (Fig. 6b–d and f). Also, *P. pallida* seedlings of the same size differed in their root length and RSR (Fig. 6b and e).

Comparisons of invasive and planted *P. juliflora* individuals

More invasive *P. juliflora* seeds germinated than plantation *P. juliflora* seeds (18% more; \( \chi^2 = 6.65, p < 0.01 \), Fig. 4a). Mean emergence time was similar between the two *P. juliflora* origins (\( \chi^2 = 0.08, p = 0.78 \), Fig. 4b), but invasive *P. juliflora* seedlings had 14% higher survival (\( \chi^2 = 10.47, p < 0.001 \), Fig. 4c). Under high water–nitrogen availability, invasive *P. juliflora* seedlings had 8% longer stems than plantation *P. juliflora* (Tukey HSD: \( p < 0.01 \), Table 2, Fig. 5b). Invasive *P. juliflora* had 32% higher stem biomass under high water availability (Tukey HSD: \( p < 0.05 \)), and under low water availability, slightly lower leave biomass (Tukey HSD:

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Figure 3. Growth responses measured as (a) height, (b) stem diameter and (c) number of stems of seedlings of invasive *P. juliflora* (red), plantation *P. juliflora* (blue) and plantation *P. pallida* (green) grown in reciprocal transplant experiments in invaded and plantation sites. Separate models were used: one between tree species (i.e. plantation *P. juliflora* and plantation *P. pallida*) and a second between *P. juliflora* origins (i.e. invasive *P. juliflora* and plantation *P. juliflora*). Bars represent mean ± standard error.

Figure 4. Early growth responses of invasive *P. juliflora* (red), plantation *P. juliflora* (blue) and plantation *P. pallida* (green) seedlings under glasshouse conditions measured as (a) percentage germination, (b) mean emergence time (MET) and (c) percentage seedling survival. Separate comparison were made: one between tree species (i.e. plantation *P. juliflora* and plantation *P. pallida*) and a second between *P. juliflora* origins (i.e. invasive *P. juliflora* and plantation *P. juliflora*). Bars represent mean ± standard error. Statistical significance: *, \( p < 0.05 \); **, \( p < 0.01 \); ***, \( p < 0.001 \) (\( p < 0.05 \); \( \chi^2 \) tests).
Figure 5. Growth responses of invasive *P. juliflora* (red), plantation *P. juliflora* (blue) and plantation *P. pallida* (green) in response to different water and nitrogen treatments measured as (a) root length, (b) stem length, (c) root biomass, (d) stem biomass, (e) root:shoot ratio (RSR), (f) leaf biomass, (g) total plant biomass and (h) number of leaves. Separate comparisons were made: one between tree species (i.e. plantation *P. juliflora* and plantation *P. pallida*) and a second between origin of *P. juliflora* (i.e. invasive *P. juliflora* and plantation *P. juliflora*). Bars represent mean ± standard error. Asterisks indicate a significant effect of the main fixed factor or an interaction with one or both water and nitrogen treatments for comparisons between tree species (black asterisks) or *P. juliflora* origins (red asterisks). In all models fixed factors water treatment and nitrogen treatment had a significant effect on the response variables (p < 0.05; F–χ² tests).
p = 0.05), and 22% less leaves (Tukey HSD: p < 0.05), compared with plantation P. juliflora (Table 3, Fig. 5d, f and h, respectively).

Overall, invasive P. juliflora showed higher plasticity compared with plantation P. juliflora (Table 3). Compared with plantation P. juliflora individuals, invasive P. juliflora individuals of bigger size also have proportionally longer stems (this difference was marginally significant when excluding outliers; p = 0.06), and allocated proportionally more biomass to stems (Fig. 6b and d).
Discussion

The invasiveness of species may stem from a combination of pre-adapted traits of ecological importance, their plasticity and rapid evolutionary changes post-introduction (Colautti and Lau 2015, Gallagher et al. 2015). We hypothesized that planted individuals of *Prosopis juliflora* and *P. pallida* differ in functional traits, their plasticity and allometric growth allocation, supportive of differences in their invasiveness. We also hypothesized that these differences exist between planted and invasive individuals of *P. juliflora*, supportive of rapid evolution during invasion. We found support for both hypotheses by showing that the means of, and plasticity in, key performance traits differ between planted *Prosopis* species that differ in their invasiveness, and that invasive *P. juliflora* individuals have diverged from those originally planted in the study area.

The traits that differentiate invasive and non-invasive species often depend on conditions in the new range (van Kleunen et al. 2010b, Kueffer et al. 2013) and/or the stage of invasion (Richardson and Pyšek 2012, Catford et al. 2019, Milanović et al. 2020). Despite these context-dependencies, species traits that underlie high performance in the native range can confer pre-adaptations to become invasive (van Kleunen et al. 2010b). For instance, root-to-shoot ratio has been put forward as an important trait for seedling performance and biomass production, particularly under drought conditions (Lloret et al. 1999). Increased allocation to roots may increase uptake, or more efficient use of, water and other soil resources during dry periods (Padilla and Pugnaire 2007). Conversely, less allocation to above-ground biomass translates into less transpiration, and thus less water loss. Rapid development of roots after germination, leading to high RSRs has been previously reported from both *Prosopis* species we studied (Pasićznik et al. 2001). In our glasshouse experiment, we found that the offspring of plantation *P. juliflora* had higher RSRs compared to those of plantation *P. pallida*. Also, plantation *P. pallida* seedlings of the same size differed in their root length but in both plantation *P. pallida* and *P. juliflora* the allocation of biomass to roots was proportionally the same. This is probably due to differences in root architecture (i.e. root diameter, root proliferation) or physiological traits not evaluated in our study. Our data suggest that differences between planted *P. juliflora* and *P. pallida* in strategies and (likely preadapted) traits related to resource use and acquisition may explain their differential invasiveness in Baringo, and could be particularly important in invasive species of arid and semi-arid systems (Funk 2013).

Among the ecological attributes that have been linked to plant invasiveness (van Kleunen et al. 2010b, Gallagher et al. 2015, Gioria and Pyšek 2017), increased height and above-ground biomass production often seem to benefit invasion success (Pyšek and Richardson 2007, van Kleunen et al. 2010b). We found the offspring of plantation *P. pallida* to be, on average, taller than those of plantation *P. juliflora* in both our transplant and glasshouse experiments. As for many trees, above-ground biomass production is positively correlated with stem diameter in *Prosopis* (Muturi et al. 2011). Therefore, even though *P. pallida* grew taller in transplant sites, *P. juliflora* likely produced more above-ground biomass due to its thicker stems. In our glasshouse experiment, and across plant sizes, plantation *P. pallida* grew longer stems and allocated more biomass to them (per unit of total plant biomass produced) compared with plantation *P. juliflora*. However, this was not linked to higher stem biomass in *P. pallida*. We also found that the offspring of planted *P. juliflora* individuals produced more stems than those of *P. pallida*. The development of numerous stems could be related to stress tolerance under low moisture availability (Pasićznik et al. 2001) and multi-stemmed plants can survive, and continue growing, if one stem dies (Götmark et al. 2016). This trait may therefore further promote the invasiveness of *P. juliflora*.

Our finding of longer emergence time in *P. juliflora* compared with plantation *P. pallida* disagrees with the general consensus that invasive species germinate earlier than non-invasive congeners (Gioria and Pyšek 2017). However, we found that early emergence was not related to survival of seedlings of both species. Early germination would also allow individuals to reach larger sizes when becoming reproductive (Donohue et al. 2010), which could be the case for *P. pallida*. Future studies should evaluate the long-term benefits of early germination such as higher establishment during late seedling development, size or fecundity in trees (Gioria et al. 2018).

Invasive plants are often liberated from their specialist natural enemies (i.e. the enemy release hypothesis; Keane and Crawley 2002) leading to higher growth and reproduction in their new ranges. The absence of specialist enemies may also create opportunities for the reallocation of (often costly) resources associated with defence strategies towards performance via rapid evolution, in what has been termed the ‘evolution of increased competitive ability (EICA)’ hypothesis (Blossey and Nötzel 1995, Bossdorf et al. 2005, Rotter and Holeski 2018). In Baringo County, we found *Prosopis* pods to be attacked by a number of seed-feeding insects. The fact that plantation *P. juliflora* individuals had significantly less damaged seeds than *P. pallida* individuals suggests that *P. juliflora* is experiencing higher levels of enemy release than *P. pallida*. These differences in enemy loads could result in differences in the survivorship, fecundity, biomass or other demographic parameters, i.e. performance, of these tree species.

Phenotypic plasticity is also often linked to plant invasion success (Gallagher et al. 2015, Huang et al. 2015), partly because individuals with higher plasticity levels would be better equipped to survive and reproduce under heterogenous environmental conditions (Richards et al. 2006). However, phenotypic plasticity does not always benefit invasion (Palacio-López and Gianoli 2011) or it may only be important during the initial stages of establishment (Bossdorf et al. 2005, Lande 2015), as plastic responses may not always translate into higher fitness (Davidson et al. 2011). Our results provide evidence to suggest that differences in phenotypic plasticity between *P. juliflora* and *P. pallida* in growth responses to resource availability, can separate invasive and non-invasive species. We found the offspring of invasive *P
juliflora individuals to also differ in allometric growth allocation from those of planted individuals in stem length and stem biomass (Fig. 6). Despite the possible contributions of genetic variation to these differences, they do support the differences we observed in phenotypic plasticity between these two groups (sensu Xie et al. 2015). It is therefore possible that phenotypic plasticity also contributed to the invasive spread of P. juliflora in Baringo. The fact that invasive P. juliflora individuals increased growth in response to high resource availability, compared to planted individuals, agrees with studies on various invasive plants yielding similar findings (Daehler 2003, Catford et al. 2009, Sun and Roderick 2019).

Our comparison between the offspring of planted P. juliflora individuals (i.e. ancestors) and their invasive descendants, also provides evidence for rapid post-introduction evolution during invasion, indicated by trait differentiation and differences in plasticity and allometric growth responses between them. Invasive species frequently undergo rapid evolution, often in response to abrupt changes host plant or food resources, the bio-physical environment, mortality rates and competitive interactions (Reznick and Ghalambor 2001, Moran and Alexander 2014, van Kleunen et al. 2018, Reznick et al. 2019). We found the offspring of invasive P. juliflora individuals to have larger seeds, more seeds per pod, as well as higher germination and seedling survival rates than those of planted individuals. Moreover, towards the end of our reciprocal transplant experiment (i.e. after 17 months), we observed the onset of maturity in the offspring of invasive P. juliflora, but not in any of the offspring of the original planted individuals. Proopsis seeds are dispersed mainly by water and animals (Pasiecznik et al. 2001) and bigger seeds are generally more likely to establish once dispersed (Westoby et al. 1996). A recent meta-analysis found that woody plants produced denser seed banks in their non-native than in their native ranges (Gioria et al. 2019), suggesting greater seed production and/or lower seed predation or mortality in the non-native than in the native range. It is not easy to explain the mechanisms and processes underlying such observations. For example, some seed traits are highly variable and can evolve rapidly under environmental uncertainty (Donohue et al. 2005, Donohue et al. 2010). On the other hand, differences in the (a)biotic conditions between native and non-native ranges can translate into differences in seed production and germination rates due to phenotypic plasticity or adaptive responses. Our comparisons suggest rapid evolution in the new range as the most likely mechanism for the differences we observed in the size, number and fecundity of seeds between planted and invasive P. juliflora.

Molecular studies have only identified rare instances of inter-specific hybridization. Alternatively, differences in traits affecting dispersal, either directly through the movement of seed, or indirectly through the increased survival of dispersed seeds, may have influenced the range expansion of P. juliflora in Kenya, leading to so-called spatial sorting (sensu Shine et al. 2011). Spatial sorting during rapid range expansions can increase the relative dominance of ‘fitter’ dispersive individuals at the invasion front compared to the core range. While empirical evidence for spatial sorting during remains scant, studies on plants (Tabassum and Leishman 2018) and animals (Shine et al. 2011, Berthouly-Salazar et al. 2012, Clarke et al. 2019) illustrate that it often leads to rapid micro-evolutionary change during invasion.

While our research provides evidence for rapid post-introduction evolution in invasive P. juliflora, we found little support for the notion that this has led to local adaptation. Local adaptation would imply a specific form of origin of P. juliflora–by-transplant site (plantation or invaded) interaction in our models (Kawecki and Ebert 2004, Colautti and Barrett 2013). That is, in each habitat P. juliflora of local origin (i.e. ‘home’ individuals) is expected to have higher fitness than P. juliflora from another habitat (i.e. ‘foreign’ individuals) (sensu Colautti and Barrett 2013). While we found differences between planted and invasive P. juliflora individuals, it is maybe unsurprising that we did not find such an interaction, as one would not expect planted P. juliflora individuals to be locally adapted to plantation conditions, since they found themselves in a new environment purely as a result of having been planted there.

Overall, our findings suggest that ecological and evolutionary processes can act in synergy to determine species invasiveness. We provide evidence to suggest that differences in only a few key performance traits, and their plasticity, may be enough to determine whether congeners become invasive or not. These findings have important management implications since alien trees for wood and fodder production in arid and semiarid zones are often selected based on their traits like fast growth rates, drought resistance, high seed production and hardiness, all of which may also promote invasiveness (Brundu et al. 2020). Our study also shows that direct comparisons between founding and invasive individuals, which avoids complications related to a comparison of populations from the native and the invaded range (Colautti and Lau 2015), can allow detection of rapid evolution during invasion, even for organisms like Proopsis trees with relatively long generation times.

Author contributions

Maria L. Castillo: Conceptualization (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Writing – review and editing (equal). Urs Schaffner: Conceptualization (equal); Methodology (supporting); Project administration (equal); Supervision (supporting); Writing – review and editing (equal). Brian W. van Wilgen: Project administration (supporting); Writing – review and editing (supporting). Johannes J. Le Roux: Conceptualization; Formal analysis (equal); Project administration (lead); Supervision (lead); Writing – original draft (equal); Writing – review and editing (equal).
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Data availability statement

Data are available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.vq83bk3s1>).

References

Barrett, S. C. H. et al. 2008. Plant reproductive systems and evolution during biological invasion. – Mol. Ecol. 17: 373–383.

Bates, D. et al. 2017. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.1-7, <http://lme4.r-forge.r-project.org/>.

Berthouly-Salazar, C. et al. 2012. Spatial sorting drives morphological variation in the invasive bird, Acridotheris tristis. – PLoS One 7: e38145.

Blussey, B. and Nötzold, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. – J. Ecol. 83: 887–889.

Bossdorf, O. et al. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. – Oecologia 144: 1–11.

Brundu, G. et al. 2020. Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. – NeoBiota 61: 65–116.

Castillo, M. L. 2019. Process and drivers of Prosopis invasions in eastern Africa. – Stellenbosch Univ., Stellenbosch, South Africa.

Castillo, M. L. et al. 2021. Genetic insights into the globally invasive and taxonomically problematic tree genus Prosopis. – AoB Plants 13: plaa069.

Catford, J. A. et al. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. – Divers. Distrib. 15: 22–40.

Catford, J. A. et al. 2019. Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. – Ecol. Lett. 22: 593–604.

Choe, S. K. et al. 2002. Status and impact of Prosopis in Kenya. Unpublished Technical Report.

Clarke, G. S. et al. 2019. May the (selective) force be with you: spatial sorting and natural selection exert opposing forces on limb length in an invasive amphibian. – J. Evol. Biol 32: 994–1001.

Colautti, R. I. and Barrett, S. C. H. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. – Science 342: 364–366.

Colautti, R. I. and Lau, J. A. 2015. Contemporary evolution during invasion: evidence for differentiation, natural selection and local adaptation. – Mol. Ecol. 24: 1999–2017.

Colautti, R. I. et al. 2006. Propagule pressure: a null model for biological invasions. – Biol. Invas. 8: 1023–1037.

Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. – Annu. Rev. Ecol. Evol. Syst. 34: 183–211.

Davidson, A. M. et al. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. – Ecol. Lett. 14: 419–431.

Donohue, K. et al. 2005. The evolutionary ecology of seed germination of Arabidopsis thaliana: variable natural selection on germination timing. – Evolution 59: 758–770.

Donohue, K. et al. 2010. Germination, postgermination adaptation and species ecological ranges. – Annu. Rev. Ecol. Evol. Syst. 41: 293–319.

Eckert, S. et al. 2020. Niche change analysis as a tool to inform management of two invasive species in eastern Africa. – Ecosphere 11: e02987.

Enders, M. et al. 2018. Drawing a map of invasion biology based on a network of hypotheses. – Ecosphere 9: e02146.

Enders, M. et al. 2020. A conceptual map of invasion biology: integrating hypotheses into a consensus network. – Global Ecol. Biogeogr. 29: 978–991.

Funk, J. L. 2013. The physiology of invasive plants in low-resource environments. – Conserv. Physiol. 1: cot026.

Gallagher, R. V. et al. 2015. Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. – Conserv. Biol. 29: 360–369.

Geesing, D. et al. 2000. Influence of mesquite Prosopis glandulosa on soil nitrogen and carbon development: Implications for global carbon sequestration. – J. Arid Environ. 45: 157–180.

Gioria, M. and Pyšek, P. 2017. Early bird catches the worm: germination as a critical step in plant invasion. – Biol. Invas. 19: 1055–1080.

Gioria, M. et al. 2018. Timing is everything: does early and late germination favor invasions by herbaceous alien plants? – J. Plant Ecol. 11: 4–16.

Gioria, M. et al. 2019. Managing invasions by terrestrial alien plants in Ireland: challenges and opportunities. – Proc. R. Ir. Acad. 119B: 37–61.

Goodwin, B. J. et al. 1999. Predicting invasiveness of plant species based on biological information. – Conserv. Biol. 13: 422–426.

Görtsmark, F. et al. 2016. Why be a shrub? A basic model and hypotheses for the adaptive values of a common growth form. – Front. Plant Sci. 7: 1–14.

Heger, T. and Jeschke, J. M. 2018. Enemy release hypothesis. – In: Jeschke, J. M. and Heger, T. (eds), Invasion biology: hypotheses and evidence. CABJ, pp. 92–102.

Huang, Q. Q. et al. 2015. Stress relief may promote the evolution of greater phenotypic plasticity in exotic invasive species: a hypothesis. – Ecol. Evol. 5: 1160–1177.

Johansson, S. 1990. Controlling and containing the spreading of Prosopis spp. at Bura. An outline of options and required actions. Research component in Bura fuelwood project. – Tech. Rep., KEFRI, Kenya.

Kassilly, F. N. 2002. Forage quality and camel feeding patterns in central Baringo, Kenya. – Livest. Prod. Sci. 78: 175–182.

Kawecki, T. J. and Ebert, D. 2004. Conceptual issues in local adaptation. – Ecol. Evol. 7: 1225–1241.

Keane, R. M. and Crawley, M. J. 2002. Exotic plant invasions in eastern Africa. – Stellenbosch Univ., Stellenbosch, South Africa.

Keller, S. R. and Taylor, D. R. 2008. History, chance and adaptation during biological invasion: separating stochastic pheno-
typic evolution from response to selection. – Ecol. Lett. 11: 852–866.

Kueffer, C. et al. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. – New Phytol. 200: 615–633.

Lande, R. 2015. Evolution of phenotypic plasticity in colonizing species. – Mol. Ecol. 24: 2038–2045.

Liao, H. et al. 2016. How much do phenotypic plasticity and local genetic variation contribute to phenotypic divergences along environmental gradients in widespread invasive plants? A meta-analysis. – Oikos 125: 905–917.

Linders, T. E. W. et al. 2019. Direct and indirect effects of invasive species: biodiversity loss is a major mechanism by which an invasive tree affects ecosystem functioning. – J. Ecol. 107: 2660–2672.

Linders, T. E. W. et al. 2021. Stakeholder priorities determine the impact of an alien tree invasion on ecosystem multifunctionality. – People Nat., in press.

Lloret, F. et al. 1999. Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. – Funct. Ecol. 13: 210–216.

Maron, J. L. et al. 2007. Rapid evolution of an invasive species. – Ecol. Monogr. 74: 261–280.

Mbabaui, P. R. et al. 2019. Spatial evolution of Prosopis invasion and its effects on ULC and livelihoods in Baringo, Kenya. – Remote Sens. 11: 1217.

Milanović, M. et al. 2020. Trait–environment relationships of plant species at different stages of the introduction process. – NeoBiota 58: 55–74.

Moran, E. V. and Alexander, J. M. 2014. Evolutionary responses to global change: lessons from invasive species. – Ecol. Lett. 17: 637–649.

Muturi, M. et al. 2011. Allometric equations for estimating biomass in naturally established Prosopis stands in Kenya. – J. Hortic. For. 4: 69–77.

Novoa, A. et al. 2020. Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. – Biol. Invas. 22: 1801–1820.

Otsamo, A. and Maua, J. O. 1993. Observations on pod production of planted Prosopis juliflora. – E. Afr. Agr. For. J. 58: 111–114.

Owen, R. B. et al. 2004. Swamps, springs and diatoms: wetlands of the semi-arid Bogoria-Baringo Rift, Kenya. – Hydrobiology 518: 59–78.

Padilla, F. M. and Pugnaire, F. I. 2007. Rooting depth and soil moisture control Mediterranean woody seedling survival during drought. – Funct. Ecol. 21: 489–495.

Palacio-López, K. and Gianoli, E. 2011. Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a meta-analysis. – Oikos 120: 1393–1401.

Pasecnik, N. M. et al. 2001. The Prosopis juliflora – Prosopis pallida complex: a monograph. – HDRA, Coventry, UK.

Perkins, T. A. et al. 2013. Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. – Ecol. Lett. 16: 1079–1087.

Pinheiro, J. et al. 2017. nlme: linear and nonlinear mixed effects models. – R package ver. 3.1-131, <http://cran.r-project.org/web/packages/nlme/nlme.pdf>.

Prentis, P. J. et al. 2008. Adaptive evolution in invasive species. – Trends Plant Sci. 13: 288–294.

Pyšek, P. and Richardson, D. M. 2007. Traits associated with invasiveness in alien plants: where do we stand? – In: Nentwig, W. (ed.), Biological invasions. Springer, pp. 97–125.

Rejmanek, M. and Richardson, D. M. 1996. What attributes make some plant species more invasive? – Ecology 77: 1655–1661.

Reznick, D. N. and Ghalambor, C. K. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. – Genetic 112: 183–198.

Reznick, D. N. et al. 2019. From low to high gear: there has been a paradigm shift in our understanding of evolution. – Ecol. Lett. 22: 233–244.

Richards, C. L. et al. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. – Ecol. Lett. 9: 981–993.

Richardson, D. M. and Pyšek, P. 2012. Naturalization of introduced plants: ecological drivers of biogeographical patterns. – New Phytol. 196: 383–396.

Rogers, W. E. and Siemann, E. 2004. Invasive ecotypes tolerate herbivory more effectively than native ecotypes of the Chinese tallow tree Sapium sebiferum. – J. Appl. Ecol. 41: 561–570.

Roter, M. C. and Holeski, L. M. 2018. A meta-analysis of the evolution of increased competitive ability hypothesis: genetic-based trait variation and herbivory resistance tradeoffs. – Biol. Invas. 20: 2647–2660.

Schlichting, C. D. and Levin, D. A. 1986. Phenotypic plasticity: an evolving plant character. – Biol. J. Linn. Soc. 29: 37–47.

Schriever, K. et al. 2017. Adaptive and non-adaptive evolution of trait means and genetic trait correlations for herbivory resistance and performance in an invasive plant. – Oikos 126: 572–582.

Shackleton, R. T. et al. 2014. Prosopis: a global assessment of the biogeography, benefits, impacts and management of one of the world’s worst woody invasive plant taxa. – AoB Plants 6: plu027.

Shine, R. et al. 2011. An evolutionary process that assembles phenotypes through space rather than through time. – Proc. Natl Acad. Sci. USA 108: 5708–5711.

Sokal, R. R. and Rohlf, F. J. 1995. Biometry: the principles and practice of statistics in biological research, Vol. 887. – WH Freeman.

Sun, Y. and Roderick, G. K. 2019. Rapid evolution of invasive traits facilitates the invasion of common ragweed, Ambrosia artesiiifolia. – J. Ecol. 107: 2673–2687.

Tabassum, S. and Leishman, M. R. 2018. Have your cake and eat it too: greater dispersal ability and faster germination towards it too: greater dispersal ability and faster germination towards range edges of an invasive plant species in eastern Australia. – Biol. Invas. 20: 1199–1210.

Valladares, F. et al. 2002. Plasticity, instability and canalization: is the phenotypic variation in seedlings of sclerophyll oaks consistent with the environmental unpredictability of Mediterranean ecosystems? – New Phytol. 156: 457–467.

Valladares, F. et al. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. – J. Ecol. 94: 1103–1116.

van Kleunen, M. et al. 2010a. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. – Ecol. Lett. 13: 947–958.
van Kleunen, M. et al. 2010b. A meta-analysis of trait differences between invasive and non-invasive plant species. – Ecol. Lett. 13: 235–245.
van Kleunen, M. et al. 2018. The ecology and evolution of alien plants. – Annu. Rev. Ecol. Evol. Syst. 49: 25–47.
Warton, D. and Ormerod, J. 2007. Smatr:(Standardised) major axis estimation and testing routines. – R package ver. 2.0, <www.bio.mq.edu.au/ecology/SMATR/>.
Westoby, M. et al. 1996. Comparative ecology of seed size and dispersal. – Phil. Trans. R. Soc. B 351: 1309–1318.
Wilson, J. R. U. et al. 2007. Residence time and potential range: crucial considerations in modelling plant invasions. – Divers. Distrib. 13: 11–22.
Xie, J.-B. et al. 2015. Apparent plasticity in functional traits determining competitive ability and spatial distribution: a case from desert. – Sci Rep. 5: 1–18.
Zenni, R. D. et al. 2014. Rapid evolution and range expansion of an invasive plant are driven by provenance–environment interactions. – Ecol. Lett. 17: 727–735.