






Research Article

Native and invasive seedling drought-resistance under elevated temperature in common gorse populations

Mathias Christina^{1,2,3,*}, Céline Gire¹, Mark R. Bakker¹, Alan Leckie⁴, Jianming Xue⁴, Peter W. Clinton⁴, Zaira Negrin-Perez⁵, José Ramon Arevalo Sierra⁵, Jean-Christophe Domec¹ and Maya Gonzalez¹

¹INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, F-33882 Villenave-d'Ornon, France, ²CIRAD, PERSYST Department, UPR 115 AIDA, 97490 Sainte-Clotilde, La Reunion, France, ³AIDA, PERSYST Department, Univ Montpellier, CIRAD, Montpellier, France, ⁴New Zealand Forest Research Institute trading as Scion, 8440 Christchurch, New Zealand, ⁵Department of Botany, Ecology and Plant Physiology, University of La Laguna, 38206 La Laguna, Spain

*Corresponding author. E-mail: mathias.christina@cirad.fr

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Abstract

The assumption that climatic growing requirements of invasive species are conserved between their native and non-native environment is a key ecological issue in the evaluation of invasion risk. We conducted a growth chamber experiment to compare the effect of water regime and temperature on the growth and mortality of native and invasive populations of common gorse seedlings (*Ulex europaeus* L.). Seeds were sampled from 20 populations of five areas from both native (continental France and Spain) and non-native areas (New Zealand, Canary and Reunion islands). The seedlings were grown over 36 days in two temperature treatments (ambient and elevated) combined with two water treatments (irrigated or droughted). The elevated temperature (ET) was defined as the highest temperature observed at the niche margin in the different countries. While ET increased seedlings growth, the drought treatment increased mortality rate and limited seedlings growth. Under ET and drought, native populations showed a greater mortality rate (53%) than invasive populations (16%). Invasive seedlings also showed higher above- and belowground development than native ones under these constrained climatic conditions. While phenotypic plasticity did not differ between native and invasive populations, the difference between populations in terms of total dry mass could be related to differences in the climate of origin (precipitation in particular). Assessing the importance of phenotypic changes between populations within invasive species is crucial to identify the margins of their climatic distribution range and to highlight areas where management efforts should be concentrated in order to limit its spread.

Keywords invasion, alien plants, drought, climatic niche, establishment

普通金雀花种群在高温下的本土和入侵幼苗抗旱性

摘要：入侵物种的气候生长需求在其本土和非本土环境之间保持一致的假设是评估入侵风险的关键生态学问题。本研究通过生长箱实验，比较水分和温度对普通金雀花幼苗(*Ulex europaeus* L.)本土种群和入侵种群生长和死亡率的影响。从本土(法国大陆和西班牙)和非本土(新西兰、加那利群岛和留尼旺岛)的5个地区的20个种群中采集了种子样本。幼苗在两种温度处理(环境温度和高温)和两种水处理(灌溉和干旱)中

生长超过36天。温度升高被定义为在不同国家的生态位边缘观察到的最高温度。虽然温度升高增加了幼苗的生长，但干旱处理增加了死亡率并限制了幼苗的生长。在高温和干旱条件下，本土种群的死亡率(53%)高于入侵种群(16%)。在这些受限的气候条件下，入侵幼苗的地上和地下发育也好于本土幼苗。虽然表型可塑性在本土种群和入侵种群之间没有差异，但种群之间总干物质生物量的差异可能与起源气候(尤其是降水)的差异有关。评估入侵物种种群之间表型变化的重要性对于确定其气候分布范围的边缘以及对突出应集中管理以限制其传播的区域都至关重要。

关键词：入侵，外来植物，干旱，气候生态位，定植

INTRODUCTION

Biological invasion is a major economic and environmental ecosystem threat and is amplified by global change (Clements *et al.* 2022; Ziska 2022). The invasion of islands by plant species is currently a serious threat to endemic species (Brock and Daehler 2022). The assumption that climatic requirements of invasive species are conserved between their native and invaded range is key in assessing and quantifying invasive risk (Bates *et al.* 2020; Pearman *et al.* 2008). However, this hypothesis is not fully supported. Even though a review concluded that ~85% of terrestrial invasive plants would not be able to shift their climatic niche (Petitpierre *et al.* 2012), evidence of climatic niche shifts has been shown for specific invasive plants (Broennimann *et al.* 2007; Zachariah Atwater and Barney 2021). In particular, Webber *et al.* (2012) and Liu *et al.* (2020) suggested that niche conservatism for invasive species would be the exception rather than the rule. For the efficient allocation of management resources, we need to improve our characterization of exotic species' ecological and climatic niches both in their native and invasive environments, so we can understand which factors limit or even prevent the establishment and spread of these species (Leung *et al.* 2002).

Understanding how genetic variation in invasive plants influence climatic niche shifts is becoming crucial under rapid climate change (Colautti *et al.* 2017). Climatic niche shifts could occur when change in plant fitness differs between native and invasive individuals or populations from the same species which could result from phenotypic divergences in plant traits influencing survival and reproduction (Funk *et al.* 2017). In such case, it suggests that invasive populations are adapted to a wider climatic environmental range than native ones, and thus better fit to colonize larger areas. Even though local adaptation of populations is not observed in all invasive species (Li *et al.* 2015; VanWallendael *et al.*

2018), invasive species often present rapid evolution and a high-genetic variation, thus enabling rapid local adaptation to new ecosystems (Colautti and Barrett 2013; Colautti *et al.* 2017). In addition, for those introduced species that spread across a wide distributional range, phenotypic plasticity has been proposed as an important contributor to invasive success (Davidson *et al.* 2011; Mounger *et al.* 2021). In particular, the phenotypic plasticity could improve survival rates during the initial establishment in a new environment (Ghalambor *et al.* 2007). However, there is still debate on the relative contribution of phenotypic plasticity and local genetic variation (i.e. local adaptation) to the ability of widespread invasive plants to colonize new environments (Liao *et al.* 2016).

A new plant species introduced outside its native range has to cross several barriers before becoming an invader (Blackburn *et al.* 2011; Richardson *et al.* 2000). An initial stage is the establishment (survival) of young seedlings, which is strongly influenced by abiotic conditions. Many findings pointed out that seedling establishment is restricted by climatic conditions such as temperature, water availability or light (Danner and Knapp 2003; Hou *et al.* 2014; Kellman 2004; Leiblein-Wild *et al.* 2014; Nguyen *et al.* 2016), particularly for high-elevation ecosystems (Arévalo *et al.* 2010; Tecco *et al.* 2016). Yet, few studies have dealt with the influence of abiotic factors on seedling establishment at the margin of its climatic niche (e.g. Eyster and Wolkovich 2021; Kellman 2004; Laube *et al.* 2015), which is crucial to understand the mechanisms of niche changes.

In this study, we tested the tolerance of an important invasive shrub (common gorse, *Ulex europaeus* L.) to two imposed abiotic factors (temperature and water availability) at the margin of its native climatic niche. Gorse is a particularly interesting model species as it is among the 32 most invasive land plant species worldwide (IUCN, Roberts and Florentine 2021) at latitudes ranging from 54° S to 60° N and at altitudes ranging from

Table 1: Gorse (*Ulex europaeus*) source population information

Range	Country	Population	Latitude	Longitude	Elevation (m)	T_{MEAN} (°C)	$T_{\text{MEAN.D.Q}}$ (°C)	PPT _{YR} (mm)	PPT _{W.Q.} (mm)	Number of individuals
Native	Spain	COM	43.283	−5.017	793	9.5	15.6	902	173	8
		MdR	43.283	−5.000	910	8.9	15.1	931	178	8
		CA	42.983	−4.233	1114	8.9	15.4	867	161	15
		LdE	43.267	−4.983	1146	8.9	15.1	931	178	6
	France	AND	44.733	−1.100	10	13.0	19.2	1049	198	22
		BPM	48.683	−1.933	10	11.4	10.4	738	173	5
		CAUD	44.567	−0.983	22	12.9	19.2	1061	202	5
		MAD	44.750	−0.400	86	12.4	19.1	934	188	9
		FSP	43.367	−1.533	98	13.6	19.3	1307	272	12
		be	48.117	−3.333	200	10.6	15.7	964	183	16
		SAR	43.333	−1.583	206	13.8	19.4	1308	272	7
Invasive	Canary	LAG	28.510	−16.322	680	16.2	19.1	552	19	12
	New-Zealand	WAI	−44.667	170.967	340	10.2	6.0	677	187	6
		RV	−41.150	173.567	400	11.2	15.6	1694	330	17
		Inw	−41.567	172.933	890	9.4	13.8	1578	323	14
	Reunion	RPP	−21.137	55.613	1100	16.8	14.5	1653	712	6
		RCA	−21.276	55.584	1290	15.6	13.3	1704	722	13
		RSI	−21.225	55.582	1620	16.0	13.7	1693	721	6
		RMB	−21.062	55.374	1850	15.2	13.0	1755	754	7
		RMM	−21.069	55.379	1990	15.7	13.4	1726	743	18

Climatic variables at each location were obtained from WorldClim: mean annual temperature (T_{MEAN}), mean temperature of the driest quarter ($T_{\text{MEAN.D.Q}}$), annual precipitation (PPT_{YR}), and precipitation of the warmest quarter (PPT_{W.Q.}). The number of individuals represents the number of seedlings used in the growth chamber experiment.

sea level to 3550 m a.s.l. (Hornoy *et al.* 2013). Its world-scale distribution suggests a potentially broad niche with respect to climatic variables (particularly temperature) with a compensatory phenomenon with soil water content and atmospheric humidity (e.g. gorse is only present at high altitude for lower latitudes). Recent modelling studies suggested that the climatic niche of introduced gorse populations changed in comparison to native populations, allowing invasive populations to invade warmer and drier environments in North America, South America and Australia (Christina *et al.* 2020; Hernández-Lambrano *et al.* 2016). Our first objective was to assess the climatic niche margins of gorse in terms of temperature and water availability as a complement to its used (realized) niche assessed in previous studies. Our second objective was to assess

the potential phenotypic differences between native and invasive seedlings traits that could explain this climatic niche shift. The hypotheses were that: (i) gorse seedling fitness is reduced in warm and dry environments, (ii) invasive gorse seedlings are more performant in warm and dry environments than in native ones and (iii) the differences in performance among gorse seedlings can be explained by intra-specific trait variability.

MATERIALS AND METHODS

Assessing the temperature niche of *Ulex europaeus* in studied countries

Ulex europaeus L. (gorse) native populations from France and Spain and invasive populations from Canary Islands, Reunion Island and New Zealand

were used in this study (Table 1). Prior to the experiment, the climatic niche of gorse was assessed in each country. Localization of gorse populations was performed in a previous study using various field reconnaissance and literature queries (Christina *et al.* 2020). In total, 2627, 1068, 5, 1005 and 457 gorse populations were located in France, Spain, Canary Islands, Reunion Island and New Zealand, respectively. The data for these populations were then transformed to a 5 arc min (~10 km) grid of gorse presence and matched with WorldClim bioclimatic variables (5 arc min, worldclim.org, version 1.4, Hijmans *et al.* 2005). We used the WorldClim bioclimatic variables to define two temperature ranges, one ambient temperature (AT) corresponding to an average temperature where gorse was present and one ET corresponding to a temperature at the margin of the temperature tolerance of gorse. Climatic data were presented using a beanplot (Kampstra 2008) based on a normal density function.

Studied populations

Seeds were sampled from 20 populations from five countries and altitudes ranging from sea level to 2000 m a.s.l. (Table 1). Eleven populations were considered as natives (seven from continental France and four from Spain) and nine populations sampled in non-native ecosystems (five from Reunion Island, three from New Zealand and one from Canary Island). In each population, 20 different individuals were selected and 50 seed pods per individuals were sampled during the reproductive period. Only mature brown pods were collected. The seeds were stored in the pods at 4°C until required. The seeds were carefully examined to exclude any seeds that had been attacked by insects. Climatic data at each location were obtained from WorldClim bioclimatic variables (2.5 arc min, worldclim.org, version 1.4, Hijmans *et al.* 2005).

Seed germination

All equipment was sterilized in an autoclave and sterile water was used. To further minimize the risk of infestation by fungi and bacteria, seed samples were washed in 2.5% sodium hypochlorite (NaOCl) for 10 min and then rinsed during 5 min in sterile water. Seeds were then scarified for 3 h using sulfuric acid concentrated at 96%, where two volumes of acid to one volume of seeds were used (Sixtus *et al.* 2003). Note that there is a high risk of creating chlorine gas

due to contact between NaOCl and sulfuric acid. After rinsing the seeds in sterile water, they were placed in petri dishes at 15 °C until germination (~2 weeks). Petri dishes were regularly humidified.

After germination, seeds were planted at 2 cm depth in individual pots (10 cm depth) and grown in a greenhouse. Potting substrate was a typical acid sandy soil representative of southern France where native gorse grows (dry moorland: 5.9–12.7 mg C g⁻¹, 0.40–0.67 mg N g⁻¹, 0.026–0.030 mg PTOT g⁻¹, 0.13–0.19 mg OxAI g⁻¹, 0.08–0.15 mg OxFe g⁻¹). At the end of the growing period, 220 homogeneous seedlings were chosen for the experiment and assigned to the four treatments (76 from seven populations in France; 40 from five populations in Spain; 12 from one population in Canary Islands; 52 from six populations in Reunion Island and 40 from five populations in New Zealand). In each country, seedlings were chosen in different populations to take into account phenotypic variability within each country. We sampled a large number of populations rather than individuals in each population to assess differences between populations rather than within populations. The seedlings were pooled by population and range (native *vs.* invasive) herein after referred to as either ‘native population’ or ‘invasive population’.

Temperature and watering treatments

Value of ET was defined as the highest temperature observed at the niche margin in the different countries, and throughout the experiment, the difference in temperature between the ET and AT was set at +6 °C. The maximum daily temperature (T_{MAX}) and the average daily temperature (T_{MEAN}) were defined based on the WorldClim maximum daily temperature of the warmest month and the daily mean temperature of the driest quarter, respectively (Fig. 1). Seedlings were grown in two environmental growth chambers (INRAE phytotron) each holding 110 pots: one AT chamber characterized by $T_{MAX} = 24$ °C, $T_{MEAN} = 17$ °C, $T_{NIGHT} = 10$ °C; and one ET chamber with $T_{MAX} = 30$ °C, $T_{MEAN} = 23$ °C, and $T_{NIGHT} = 16$ °C. In each chamber, four periods of light levels and temperatures were programmed to mimic mean summer day conditions: a night period of 12 h (T_{NIGHT} and photosynthetically active radiation—PAR = 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$), a morning and an afternoon period of 3 h each (T_{MEAN} and PAR $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$), and a high-temperature period of 6 h in the middle of the day (T_{MAX} and PAR $\approx 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$). In each chamber, relative humidity (RH) was adjusted to have similar non-limiting (low

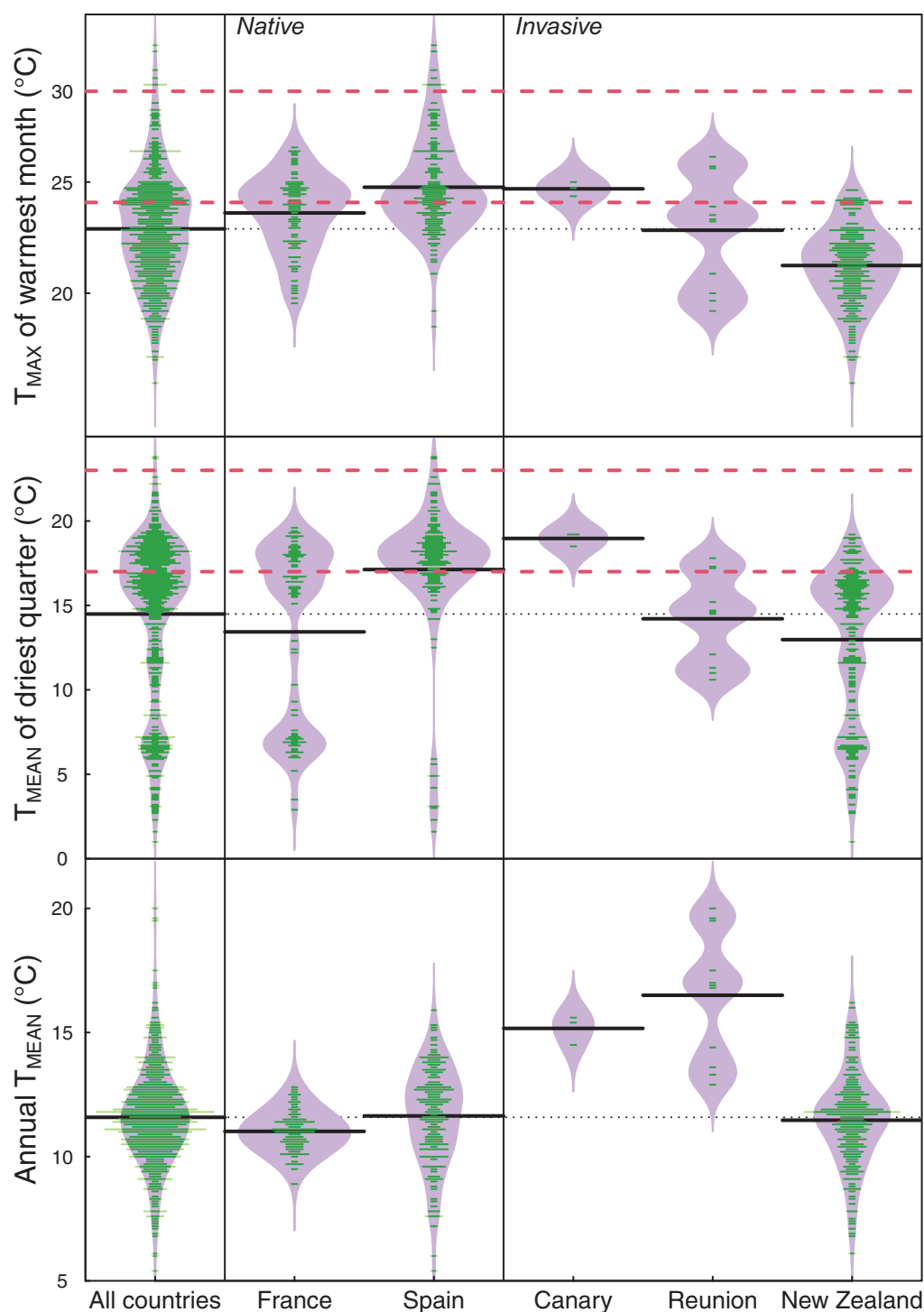


Figure 1: WorldClim climatic data where *Ulex europaeus* is present in the different studied countries (from top to bottom: maximum temperature of the warmest month, mean temperature of driest quarter and annual mean temperature) from 1960 to 1990. Data are presented using a beanplot with median (bold black lines), normal density (purple background) and populations (green short lines). The red-dashed lines represent the values used to define the elevated (ET) and ambient (AT) temperatures in the growth chamber experiment. The black-dotted lines represent the median values of all five countries.

enough) vapour pressure deficit (VPD) during the daytime. Consequently, RH in the ET chamber was set to 74% during the night and 70% during the day, corresponding to $VPD_{NIGHT} = 0.41$, $VPD_{MEAN} = 0.7$ and

$VPD_{MAX} = 1.01$ kPa periods. In the AT chamber, RH was set to 74% during the night and 60% during the day, corresponding to $VPD_{NIGHT} = 0.29$, $VPD_{MEAN} = 0.67$ and $VPD_{MAX} = 0.98$ kPa periods.

In addition, two watering treatments were applied in each chamber: one where 20 ml of water was added to each pot three times a week to maintain soil at full saturation (wet or well-watered treatment), and a drought treatment where pots were not watered over the 36-days period of the experiment (dry treatment).

Seedling growth and chamber acclimation

As described above, four treatments were applied using two controlled environment chambers (AT, wet and dry in chamber #1; ET, wet and dry in chamber #2). In this experimental design, due to a limited number of available chamber space, the temperature treatment was nested within a 'growth chamber treatment'. Nevertheless, as other climatic factors (PAR and VPD) were controlled and similar between chambers, we assume that this design was adequate to test the temperature effect. At the start of the experiment, both chambers were set up at AT and all seedlings were watered. During the first ten days, temperature of the chamber #2 increased gradually to reach the desired ET. At the end of this temperature/watering acclimation period (i.e. after ten days), and thus at the onset of the experiment, seedling heights were similar (around 19 mm; P -value = 0.59) among all native and invasive populations (Supplementary Fig. S1). Watering treatments started after this acclimation period and were maintained for 36 days.

Measurements

At the end of the 36-days period, plant traits were measured at the individual seedling level: total dry mass (T_{DM}), height (H), leaf area (LA), leaf (L_{DM}) and root dry masses (R_{DM}), root length (R_L), area (R_A) and diameter (R_D), above to belowground dry mass ratio (AB_{RATIO}), leaf to aboveground dry mass ratio (LA_{RATIO}) and specific root length (SRL) and area (SRA). Plant H was defined as the height up the apex. Note that H of a few individuals was lower after 36 days in comparison to the end of the acclimation period due to desiccation. Considering plant organs, stem, leaves/spines and roots were separated manually for each individual. Then, fresh roots and leaves were scanned (400 dpi). LA was calculated using the ImageJ software (Schneider *et al.* 2012) while R_L , R_A and R_D were calculated using the Winrhizo software (Arsenault *et al.* 1995). Stem, roots and leaves were then dried at 65 °C for three days and weighed to obtain the dry weights. Mortality rate was defined as the proportion of

dead seedlings at the end of the experiment in each population.

Seedling traits analyses

To test for phenotypic difference between invasive and native range in response to climatic variable, the effects of growth air temperature (AT vs. ET), watering treatment (wet vs. dry), population range (native vs. invasive) and their interaction on T_{DM} , H , LA, L_{DM} , R_{DM} , R_L , R_A , AB_{RATIO} , LA_{RATIO} , R_D , SLA, SRL and SRA at the individual level were tested using a linear mixed-effect model of variance (lmer function from lme4 R package). All traits were log-transformed to ensure residue normality. The model included the population identification as random effect as random effect and the population range (Inv/Nat), growth air temperature, watering treatment and their interaction, as fixed effects. The coefficient of variation of individual traits within each population in the reference treatment (AT × wet) was calculated and no difference between native and invasive populations were found (Wilcoxon test, Supplementary Table S1). A post hoc analysis of each mixed linear model was then realized using the emmeans function with a Tukey P adjustment method (R emmeans package). The comparison of mortality rate of invasive and native populations was performed using a non-parametric the Kruskal–Wallis test followed by a Dunn test (R dunn.test function from dunn.test package).

Additionally, we assessed the phenotypic plasticity of gorse traits at the population level, based on one plasticity index defined in (Valladares *et al.* 2006):

$$PI - \text{trait} = \frac{\sigma(\text{Me}(\text{trait}))}{\text{Me}(\text{trait})}$$

where $PI - \text{trait}$ is the plasticity index of a given trait, $\text{Me}(\text{trait})$ is the median trait of gorse seedlings in each treatment and population, $\sigma(\text{Me}(\text{trait}))$ the standard deviation of the median trait across treatments and $\text{Me}(\text{trait})$ the average of the median trait across treatments. Populations where all individuals died in a treatment were removed from the analysis as no $\text{Me}(\text{trait})$ could be calculated (five populations). Comparison of phenotypic plasticity index between native and invasive populations was then performed using a non-parametric Wilcoxon test.

Principal component analyses

A first principal component analyses (PCAs) was performed on the WorldClim data from the location of each studied population: mean annual

Table 2: Effect of population ranges (Inv/Nat: invasive vs. native), air temperatures (*T*: ambient vs. elevated), watering levels (*W*: wet vs. dry), and their interaction on gorse traits measured in the growth chamber experiment

Trait	Inv/Nat	<i>T</i>	<i>W</i>	<i>T</i> × <i>W</i>	Inv/Nat × <i>T</i>	Inv/Nat × <i>W</i>	Inv/Nat × <i>T</i> × <i>W</i>
<i>T</i> _{DM}	<i>F</i> = 6.8**	<i>F</i> = 0.3	<i>F</i> = 19.9***	<i>F</i> = 0.1	<i>F</i> = 0.7	<i>F</i> = 1.5	<i>F</i> = 0.3
<i>H</i>	<i>F</i> = 3.9	<i>F</i> = 92.1***	<i>F</i> = 16.0***	<i>F</i> = 12.7***	<i>F</i> = 5.8*	<i>F</i> = 1.9	<i>F</i> = 0.3
<i>LA</i>	<i>F</i> = 3.5	<i>F</i> = 22.9***	<i>F</i> = 61.9***	<i>F</i> = 3.8	<i>F</i> = 3.9*	<i>F</i> = 0.9	<i>F</i> = 0.9
<i>L</i> _{DM}	<i>F</i> = 7.2*	<i>F</i> = 1.4	<i>F</i> = 20.7***	<i>F</i> < 0.1	<i>F</i> = 0.1	<i>F</i> = 1.0	<i>F</i> = 0.7
<i>R</i> _{DM}	<i>F</i> = 4.0	<i>F</i> = 0.2	<i>F</i> = 9.0**	<i>F</i> = 0.3	<i>F</i> = 0.6	<i>F</i> = 3.2	<i>F</i> = 0.4
<i>R</i> _L	<i>F</i> = 1.6	<i>F</i> = 3.2	<i>F</i> = 10.2**	<i>F</i> = 0.3	<i>F</i> < 0.1	<i>F</i> = 8.8**	<i>F</i> = 0.4
<i>R</i> _A	<i>F</i> = 2.4	<i>F</i> = 0.5	<i>F</i> = 68.8***	<i>F</i> < 0.1	<i>F</i> = 0.4	<i>F</i> = 7.8*	<i>F</i> = 0.4
<i>R</i> _D	<i>F</i> = 0.1	<i>F</i> = 24.9***	<i>F</i> = 430.6***	<i>F</i> = 5.9*	<i>F</i> = 5.5*	<i>F</i> = 0.7	<i>F</i> < 0.1
<i>AB</i> _{RATIO}	<i>F</i> = 1.3	<i>F</i> = 0.2	<i>F</i> = 9.3**	<i>F</i> = 1.1	<i>F</i> = 0.2	<i>F</i> = 4.5*	<i>F</i> < 0.1
<i>LA</i> _{RATIO}	<i>F</i> = 0.7	<i>F</i> = 5.8*	<i>F</i> = 2.3	<i>F</i> < 0.1	<i>F</i> = 0.7	<i>F</i> = 4.6*	<i>F</i> = 2.1
<i>SLA</i>	<i>F</i> = 5.0*	<i>F</i> = 70.3***	<i>F</i> = 53.6***	<i>F</i> = 11.4***	<i>F</i> = 10.6**	<i>F</i> = 0.3	<i>F</i> < 0.1
<i>SRL</i>	<i>F</i> = 1.3	<i>F</i> = 10.0**	<i>F</i> < 0.1	<i>F</i> < 0.1	<i>F</i> = 1.3	<i>F</i> = 5.0*	<i>F</i> < 0.1
<i>SRA</i>	<i>F</i> = 1.8	<i>F</i> = 0.6	<i>F</i> = 124.9***	<i>F</i> = 1.9	<i>F</i> < 0.1	<i>F</i> = 4.3*	<i>F</i> < 0.1

Variance (*F*) analyses were performed using a linear mixed-effect model on log-transformed traits using the population of origin as random effect. *P* values were abbreviated as *, **, and *** when lower than 0.05, 0.01, and 0.001, respectively. Significant factors have been highlighted in bold.

temperature (*T*_{MEAN}), mean temperature of the driest quarter (*T*_{MEAN.D.Q}), maximum daily temperature of the warmest quarter (*T*_{MAX.W.Q}), altitude, annual precipitation (*PPT*_{YR}) and precipitation in the warmest (*PPT*_{W.Q}) and driest quarter (*PPT*_{D.Q}). A second PCA was performed on all gorse trait plasticity indices. PCAs were performed with FactoMineR and factoextra R packages. Correlation between the first two axes of the PCA and mortality rate in the AT × dry treatment and mean total dry mass per population were tested using a spearman correlation test (cor.test function). All analyses were performed using R.4.0 (R Core Team 2020). The data were deposited in INRAE dataverse (<https://data.inrae.fr/privateurl.xhtml?token=d39ec306-b226-46da-ad01-ecb7cebec458>).

RESULTS

Gorse niche temperature

Gorse niche mean annual temperature (annual *T*_{MEAN}) and temperature of the warmest month (*T*_{MAX}) differed slightly (<1 °C) between France and Spain, the two countries of origin (Fig. 1). The warmest invasive areas occupied by gorse were found in Canary Island

and Reunion Island, but invasive populations from New Zealand occupied areas with similar *T*_{MEAN} as native continental populations (France and Spain). During dry seasons warmest areas occupied by gorse could be found in both native (Spain) and invasive (Canary Island) areas.

Gorse response to air temperature and watering level

Air temperature and watering levels influenced mortality rate ($\chi^2 = 30.9$, *df* = 3, *P* < 0.001) and traits of gorse seedlings (Tables 2 and 3). Mortality rate was almost null under AT or ET with no water stress, while it reached 36% on average under the interaction of ET and drought (ET × dry, Table 3). In terms of growth, *T*_{DM} of gorse seedlings was not influenced by air temperature but was lower by 17% in the dry treatment in comparison to the wet one (Table 3). Similarly, *L*_{DM}, *R*_{DM}, *R*_L, *R*_A, *AB*_{RATIO} and *SRA* were statistically influenced by watering level but not by air temperature. Reduction in the dry treatment varied from 32% for *R*_A to 9% for *AB*_{RATIO}. *H*, *R*_D and *SLA* were influenced by the interaction between air temperature and watering level (Table 2). The tallest seedlings were found in the ET × Wet treatment with

Table 3: Mean trait values depending on air temperature (ambient—AT vs. elevated—ET), watering levels (wet vs. dry) and their interaction

Trait	Unit	AT × Wet	AT × Dry	ET × Wet	ET × Dry
Mortality rate	%	0 (±0) b	7 (±16) b	0 (±0) b	36 (±37) a
Total dry mass (T_{DM})	mg	71 (±20) a	58 (±16) b	73 (±22) a	62 (±18) b
Height (H)	mm	17.9 (±5.1) c	17.6 (±4.7) c	32.2 (±10.3) a	23.8 (±8.3) b
Leaf area (LA)	cm ²	2.86 (±1.11) b	2.09 (±0.63) c	3.97 (±1.23) a	2.55 (±0.96) bc
Leaf dry mass (L_{DM})	mg	25 (±9) ab	20 (±6) c	27 (±8) a	22 (±8) bc
Root dry mass (R_{DM})	mg	34 (±10) a	29 (±9) b	35 (±12) ab	31 (±9) ab
Root length (R_L)	m	1.93 (±0.67) a	1.60 (±0.56) b	2.05 (±0.60) a	1.82 (±0.55) ab
Root area (R_A)	cm ²	21.3 (±7.4) a	14.2 (±4.8) b	21.9 (±6.4) a	15.1 (±4.8) b
Root diameter (R_D)	mm	0.35 (±0.03) a	0.29 (±0.03) b	0.34 (±0.03) a	0.26 (±0.02) c
Above to belowground DM ratio (AB_{RATIO})		1.09 (±0.23) ab	1.03 (±0.25) b	1.14 (±0.28) a	1.00 (±0.21) b
Leaf to aboveground DM ratio (LA_{RATIO})		0.68 (±0.06) b	0.69 (±0.06) ab	0.69 (±0.05) ab	0.71 (±0.04) a
Specific leaf area (SLA)	cm ² g ⁻¹	115 (±17) b	106 (±18) c	152 (±25) a	118 (±20) b
Specific root length (SRL)	m g ⁻¹	56.5 (±11.1) a	55.8 (±9.3) a	60.6 (±10.6) a	59.2 (±9.4) a
Specific root area (SRA)	cm ² g ⁻¹	6.2 (±1.0) a	5.0 (±0.8) b	6.5 (±1.0) a	4.9 (±0.8) b

The standard deviations are indicated in parentheses and letters indicated significant differences based on a post hoc analysis of the model from Table 2 using the Tukey adjustment method.

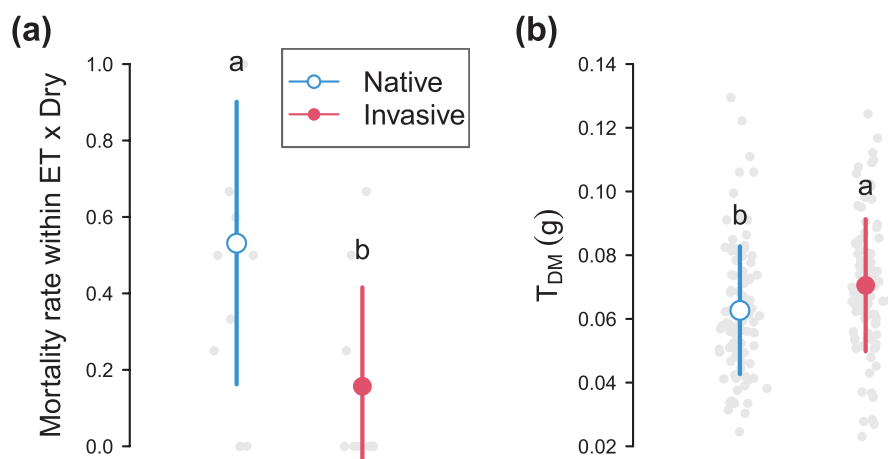


Figure 2: Change in seedling mortality rate within populations in the elevated temperature (ET) and dry temperature treatments (a) and seedling total dry mass (b) depending on population range (native vs. invasive). Means (open blue and filled red points) and standard deviations (vertical bars) are represented. Gray points represent values per population. Letters 'a' and 'b' indicate significant differences between native and invasive populations.

$H = 32$ mm, while H was 18 mm on average in the AT treatment for both watering levels. The dry treatment induced a reduction in H only when combined with ET. Similarly, the highest SLA was found in ET × Wet and SLA was lowest in AT × dry. R_D was similar in both wet AT and ET treatments. Nonetheless, R_D values were lower in the dry treatments than in the wet ones by 17% and 24% in AT and ET, respectively.

Finally, LA_{RATIO} and SRL were only influenced by air temperature and tended to be higher in ET.

Gorse mortality and total dry mass depending on population range

Seedlings from native or invasive population range responded differently in terms of gorse mortality rate and total dry mass (Table 2; Fig. 2). Within the ET ×

dry treatment, mortality rate of native populations (53%) was on average higher ($W = 78$, $P = 0.027$) than that of invasive populations (16%, Fig. 2a). The populations with the lowest mortality rates were found in Canary Islands (0%) and Reunion Island (8%, Supplementary Table S2) while mortality rate was similar among native populations (50%–53%). Considering all treatments, T_{DM} values of invasive population were higher by 11% in comparison to native populations (Fig. 2b). The country of origin had no impact on T_{DM} within each population range, all native countries and all invasive countries showed similar T_{DM} values (Supplementary Table S2).

Interaction between population range and air temperature

Among gorse traits, H , LA , R_D and SLA were significantly influenced by the interaction between population range (native vs. invasive) and air temperature (Table 2). Under AT, H of gorse from native and invasive populations was not different (Fig. 3a). Nonetheless, the increase in height under ET conditions was higher for seedlings from invasive populations (+78%) than for those from native populations (+48%). Similarly, while LA in native seedlings did not differ between AT and ET treatments, LA in invasive seedlings was 44%

higher in ET than in AT (Fig. 3b). Considering SLA , this trait was lower in invasive seedlings than in native ones under AT condition, but was similar under ET (Fig. 3c). Finally, R_D from native seedlings was slightly lower by 4% under ET than under AT conditions, while it was not different for invasive seedlings (Fig. 3d). Gorse trait values depending on country of origin are detailed in Supplementary Table S2.

Interaction between population range and watering level

AB_{RATIO} , LA_{RATIO} , R_L , R_A , SRL and SRA were significantly influenced by the interaction between population range (native vs. invasive) and watering level (wet vs. dry, Table 2). While AB_{RATIO} was constant in native seedlings whatever the watering level, AB_{RATIO} in invasive seedlings was 15% lower under dry conditions than under wet conditions (Fig. 4a). By opposition, LA_{RATIO} in invasive seedlings was 4% higher under dry than wet conditions, while it was constant in native seedlings (Fig. 4d). R_L and R_A followed a similar pattern (Fig. 4b and e). In native seedlings, R_L and R_A were lower by 27% and 41% under dry conditions compared with wet conditions. On the contrary, for invasive seedlings, R_L did not differ with watering level and R_A was only 23%

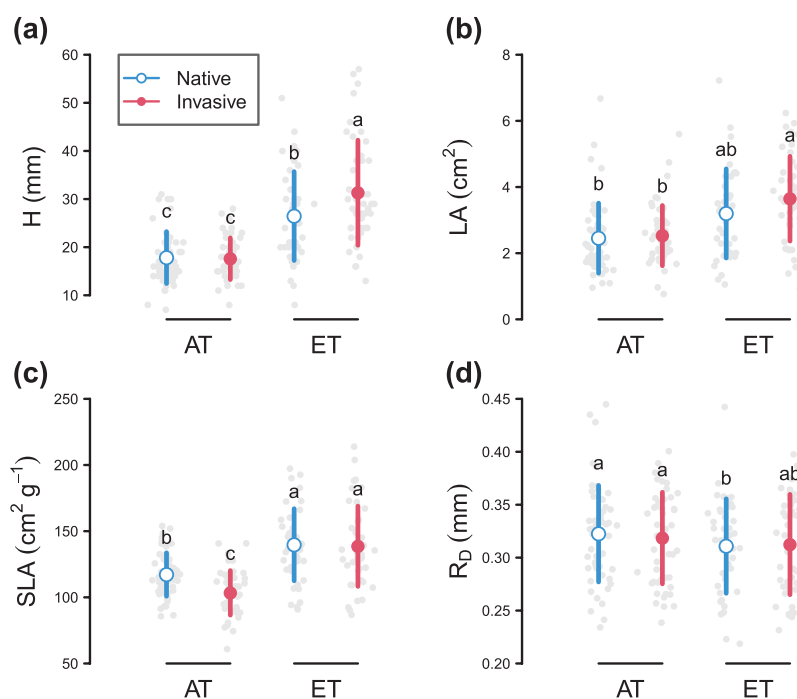


Figure 3: Change in seedling height (H , a), leaf area (LA , b), specific leaf area (SLA , c) and root diameter (R_D , d) depending on the interaction between the air temperature treatment (ambient—AT vs. elevated—ET) and the population range (native vs. invasive). Open blue and filled red points indicate the mean while the bars indicate the standard deviation. Small gray points represent values per seedlings. Letters 'a' and 'b' indicate significant differences.

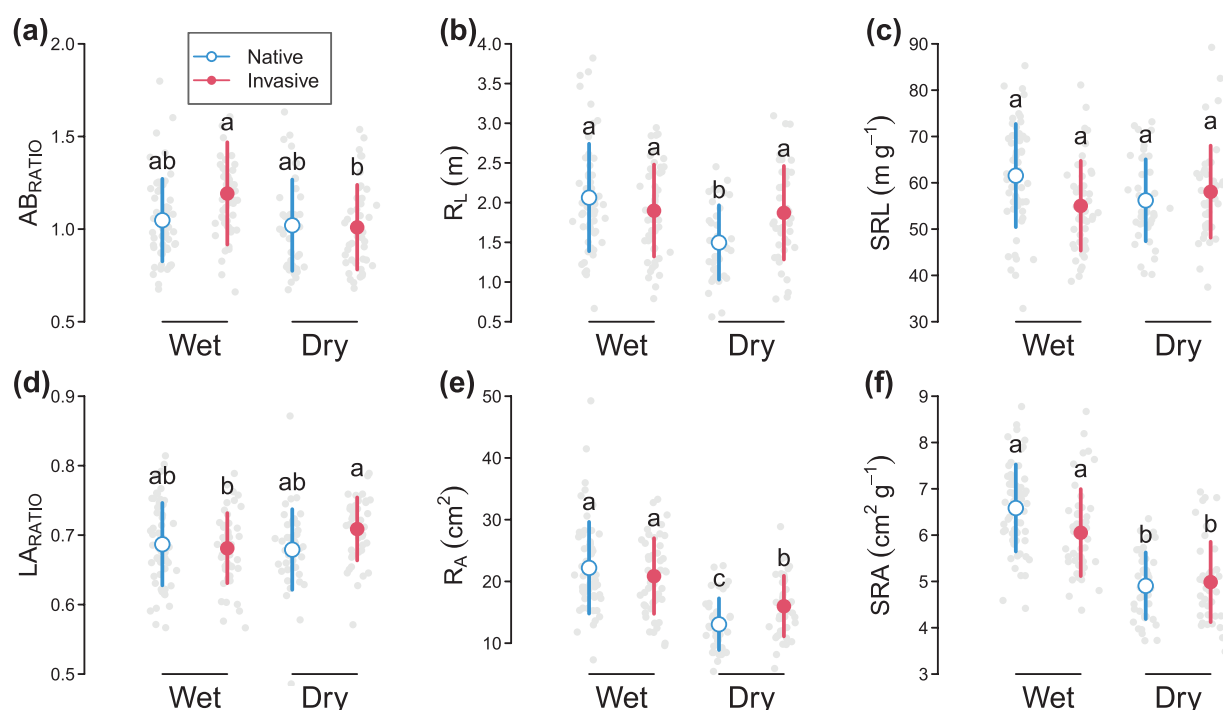


Figure 4: Change in seedling above to belowground ratio (AB_{RATIO} , **a**), root length (R_L , **b**), specific root length (SRL, **c**), leaf to aboveground ratio (LA_{RATIO} , **d**), root area (R_A , **e**) and specific root area (SRA, **f**) depending on the interaction between the watering treatment (wet vs. dry) and the population range (native vs. invasive). Open blue and filled red points indicate the mean while the bars indicate the standard deviation. Small gray points represent values per seedlings. Letters 'a' and 'b' indicate significant differences.

lower in the dry compared to the wet treatment. Finally, despite the interaction of watering level and population range being significant on SRL and SRA, no difference in the post hoc analyses could be highlighted in terms of native and invasive seedling responses (Fig. 4c and f).

Climate of origin and phenotypic plasticity

The Worldclim climate variables from population origins and the gorse trait plasticity indices were summarized into two climatic indices (CO-PC1 and CO-PC2, Fig. 5a) and two plasticity indices (PI-PC1 and PI-PC2, Fig. 5b). Considering climatic indices, the main component (CO-CI1, 44.8% of the explained variance) was mainly determined by PPT_{YR} , $PPT_{W,Q}$ and altitude while the second principal component (CO-CI2, 27.6% of the explained variance) was determined by temperature indices. While CO-CI2 did not differ depending on the population range (Fig. 5c), CO-CI1 was higher in invasive populations than native ones, highlighting different precipitation regime in native and invasive environments (Fig. 5b). Changes in each climatic index depending on population range are detailed in Supplementary Fig. S2. Seedling mortality rates were neither correlated

to CO-PC1 ($S = 1749$, $P = 0.176$) nor to CO-PC2 ($S = 1625$, $P = 0.348$). Mean total dry mass per population was not correlated to CO-PC2 ($S = 1218$, $P = 0.724$) but was significantly correlated with CO-PC1 ($\rho = 0.50$, $S = 666$, $P = 0.027$) highlighting a higher T_{DM} in populations from high-precipitation environments than from low ones. Considering plasticity indices, neither PI-PC1 nor PI-PC2 differed with population range (Fig. 5e and f). Changes in each trait plasticity index in relation to population range are detailed in Supplementary Fig. S3. Neither PI-PC1 nor PI-PC2 was correlated with seedling mortality rate or total dry mass.

DISCUSSION

Establishment at the climatic niche margin

Assessing whether the environmental niche of a species may change between different geographical areas or time periods is extremely important for predicting the spread of invasive species in the context of ongoing climate change (Clements and Jones 2021; Wan *et al.* 2017; Wang *et al.* 2022). While global temperatures rise (Walther *et al.* 2009), extreme temperature events can reduce

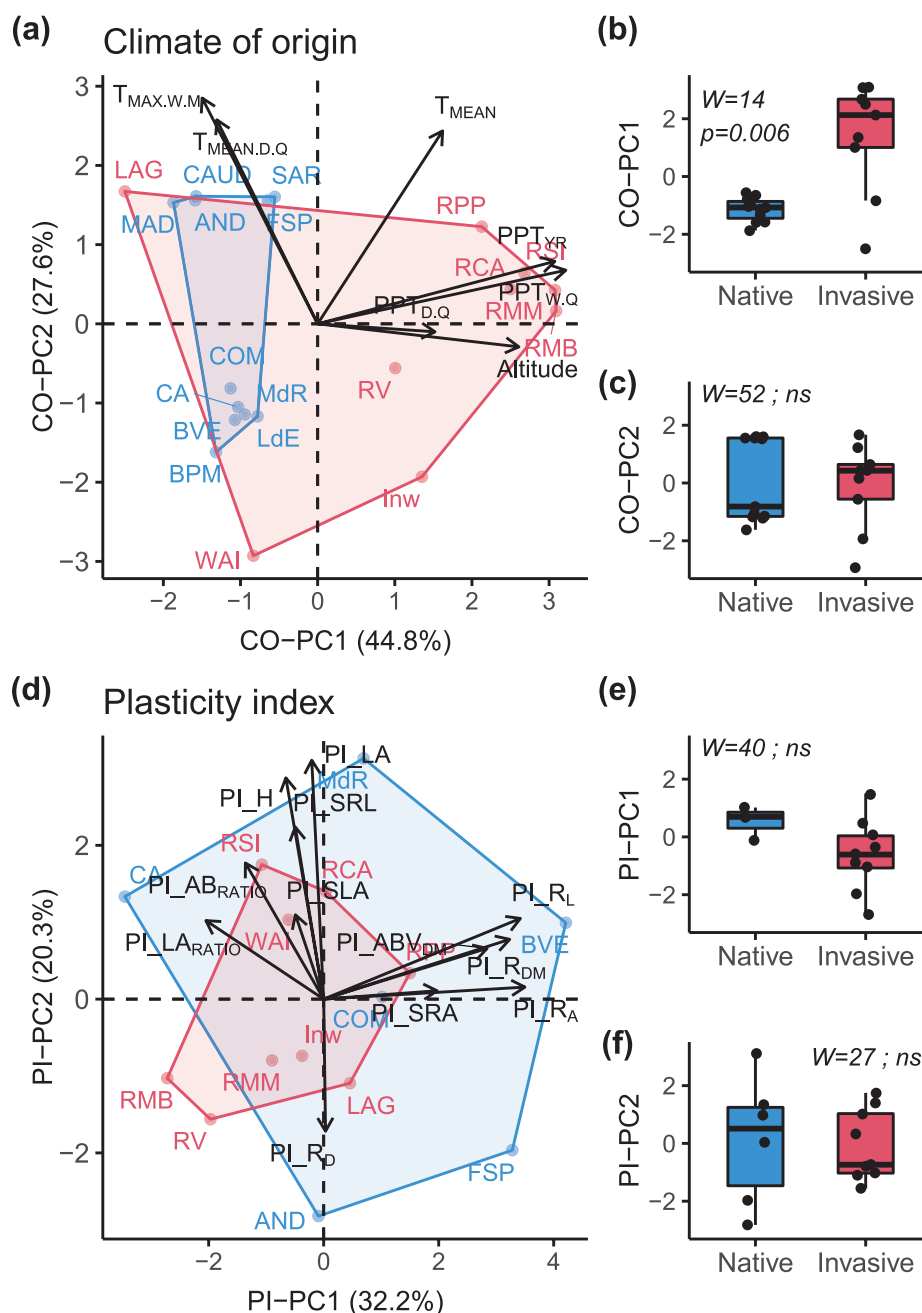


Figure 5: Principal component analyses (PCA) on climatic variables from each gorse population origin **(a)** and on plasticity indices calculated at the population level **(d)**. Climatic (extracted from WorldClim) variables were mean annual temperature (T_{MEAN}), mean temperature of the driest quarter ($T_{\text{MEAN.D.Q.}}$), maximum daily temperature of the warmest quarter ($T_{\text{MAX.W.Q.}}$), altitude, annual precipitation (PPT_{YR}) and precipitation in the warmest ($\text{PPT}_{\text{W.Q.}}$) and driest quarter ($\text{PPT}_{\text{D.Q.}}$). Trait plasticity indices were indicated as 'PI_trait'. Population identifications from Table 1 are indicated. Figures **(b)**, **(c)**, **(e)** and **(f)** represent the change in the first two PCA axis with population range (native vs. invasive). Statistical results of the Wilcoxon test (W) are provided along with P -values.

invasive plant competitiveness if conditions become unsuitable (Hellmann *et al.* 2008). Our study suggested that temperature tolerance at the thermal niche margin may change between native and invasive gorse populations. Furthermore, our

results also showed that ET in interaction with water availability can potentially facilitate the survival and reproduction of invasive gorse in regions outside its native range. In particular, the mortality rate of gorse under combined ET and drought was higher for

native seedlings than invasive seedlings (except for seedlings from New Zealand that featured a climate similar to that in the native areas; [Supplementary Table S2](#)). A similar pattern was observed in a greenhouse experiment with *Ulmus pumila* seedlings ([Hirsch et al. 2016](#)), where mortality rate of seedlings from native populations from China was greater than those from non-native populations from Argentina and the USA under various watering and temperature conditions. In its native area, gorse is an oceanic species, which makes water availability an important ecological factor shaping its niche ([Deleue et al. 2015](#)). Consequently, change in gorse seedlings' thermal and drought tolerance between invasive and native populations may be factors explaining the climatic niche shift observed at the global scale by ([Christina et al. 2020](#)) and the niche expansion of this species in South America ([Hernández-Lambraño et al. 2016](#)).

Under global change, many studies support that rising temperatures may increase the risk of invasion ([Bradley et al. 2010](#); [Walther et al. 2009](#); [Wan et al. 2017](#); [Wang et al. 2022](#)). Nevertheless, this hypothesis has to be nuanced ([Hellmann et al. 2008](#)). For example, in a meta-analysis, [Sorte et al. \(2013\)](#) showed that native and non-native plant species largely respond similarly to climate manipulations (temperature and precipitation) in terms of survival, growth or fecundity, and that, rather than simply rising temperatures, the major threat for ecosystem invasiveness comes from increasing extreme events.

Traits and seedling performance

For some plant species, this increase in vegetative growth and/or reproductive effort would result in a competitive advantage of the invasive species in the introduced ranges ([Heberling et al. 2016](#); [Ordóñez et al. 2010](#); [Wang et al. 2019](#)). In terms of vegetative growth, our study showed an increase in height and leaf area for invasive gorse populations as compared to native populations in the early phases of the invasive process (seedling establishment) under warm conditions. This observation is in accordance with previous studies showing an increase in vegetative growth ([Hornoy et al. 2011](#)) and reproductive output ([Bakker et al. 2019](#); [Udo et al. 2017](#)) in introduced *U. europaeus* populations compared to native ones under non-limiting conditions. Similar observations were also made in other invasive species such as *Rosa rugosae* (e.g. [Zhang et al. 2018](#)).

The better performance of gorse seedlings from invasive populations in extreme environments may result from change in individual traits compared

with native populations. In our study, above to belowground ratio in invasive population differed depending on watering level while it remained constant in individuals from native populations. Such differences in biomass allocation could explain the increase in drought resistance of invasive compared to native populations by allowing invasive seedlings to maintain a constant root area and length even in dry conditions, while it decreased in native seedlings. [Song et al. \(2010\)](#) found that invasive *Wedelia* (*Sphagneticola* sp. Asteraceae) seedlings suffered less inhibition in terms of growth rates due to high temperature than the native *Wedelia* (native to Central America), which was explained by a change in photosystem II activity and efficiency, as well as by higher net photosynthetic rate between native and invasive seedlings. Changes in traits that influence plant fitness under extreme conditions could explain the climatic niche shift towards warmer and drier environments observed for gorse ([Christina et al. 2020](#); [Hernández-Lambraño et al. 2016](#)).

Climate of origin and phenotypic plasticity

Invasive species often present rapid evolution ([Buswell et al. 2011](#)) and a high-genetic variation ([Laverne and Molofsky 2007](#)) which made many authors to suggest that rapid local adaptation to new ecosystems ([Colautti and Barrett 2013](#); [Colautti et al. 2017](#)) or phenotypic plasticity are key processes in the invasion success ([Davidson et al. 2011](#); [Mounger et al. 2021](#)). In the current study, we have found no difference in phenotypic plasticity at the population level between native and invasive populations for gorse seedlings when exposed to different temperature and water availability conditions. On the contrary, precipitation regime of climate of origin did differ between native and invasive populations in our study ([Fig. 5a](#)). Even though local adaptation of populations is not observed in all invasive species ([Li et al. 2015](#); [VanWallerdael et al. 2018](#)) and that some authors suggested that invasive species are not better adapted to local conditions than native ones ([Oduor et al. 2016](#)), our study showed a correlation between the dry mass of gorse populations and precipitations in the climate of origin. This result suggested a relation between the gorse population environment of origin and its growth, which could explain differences in adaptation between native and invasive gorse populations.

The evolution of phenotypic traits in invasive gorse populations has been demonstrated in common garden experiments, and has been linked to the

hexaploid karyotype of the species, and by its high-genetic polymorphism in both native and invasive populations (Hornoy *et al.* 2011, 2013). Considering that in the majority of introduced regions, invasion occurred since the 1800s (Hornoy 2012; Udo 2016), an explanation to the rapid evolution of local adaptation could result from the release of natural enemies as suggested by the evolution of increased competitive ability hypothesis (Joshi and Vrieling 2005). Indeed, the specific weevil *Exapion ulicis*, that can eat up to 80% of the gorse seeds in their native regions, was not introduced in the invaded regions as the same time as the plant (even though it has been introduced in most regions for biological control since then). The absence of this predator may have relaxed the genetic constraints resulting from the complex strategies of seed predation avoidance (Atlan *et al.* 2010), and thereby may have facilitated the rapid adaptation to new climate and contributed to the niche expansion in introduced regions (Roberts and Florentine 2021).

Study limitations and extensions

Compared to its world-scale distribution, the small amount of geographic variation captured in the introduced range may have introduced bias. Our population sampling did not cover the whole climate areas where introduced gorse can be found (Christina *et al.* 2020). Additional sampling would be required to know if our results can be generalized to other regions or if the phenotypic changes observed between native and invasive seedlings are context dependent.

The seeds used in this study come from a limited number of individuals and populations collected from the introduced and native range. The number of sample individuals was similar to previous studies comparing native and invasive populations (Eyster and Wolkovich 2021; Zhang *et al.* 2018) and should allow to incorporate a large part of the population genetic variability (Leipold *et al.* 2020). Nonetheless, the genetic variability of seeds may be higher than the genetic variability in mature gorse population, which could lead to erroneous links between seedlings phenotypic traits and change in drought and warm tolerance of invasive populations. Nevertheless, we argue that this bias should be limited considering that the trait phenotypic variability was similar between native and invasive populations (Supplementary Table S1).

Another limitation of this study comes from the vegetative growth measured at an early seedling stage

(36 days) which do not necessarily represent change in reproductive success at a later stage. Indeed, previous studies on native and invasive plant species in common garden studies have shown that increase in growth traits was not always linked to increase in reproductive traits (Colautti *et al.* 2009). In the case of gorse, a previous common garden experiment on native (La Reunion) and invasive (New Zealand) have shown a positive correlation between plant height and pod density but no difference between native and invasive populations in terms of reproductive output (seeds and pods, Hornoy *et al.* 2011). Nonetheless, this study was limited to one climatic conditions and required to be confirmed by wider reciprocal transplant experiments (e.g. Negrin-Pérez *et al.* 2018).

CONCLUSIONS

The study assessed the influence of the interaction between ET (at the niche margin) and drought on establishment success (seedling survival and growth allocation) of the invasive gorse. Our results highlight changes in seedling phenotypes related to above and belowground development between native and invasive gorse populations, which could explain the increase in drought resistance of invasive populations at extreme temperatures. A common garden approach set up by our research group, and currently taking place in both native and invasive environments along an altitudinal gradient, will allow the completion of observations in a natural environment and validate the role of phenotypic divergences into gorse expansion towards warm and dry areas around the world.

Supplementary Material

Supplementary material is available at *Journal of Plant Ecology* online.

Figure S1: Initial height (mm) after the 10-day acclimation period of gorse seedlings coming from five locations (native populations from France and Spain; invasive populations from Canary, Reunion and New Zealand islands).

Figure S2: WorldClim climatic data from localization of each gorse population depending on their population range (native vs. invasive).

Figure S3: Gorse trait plasticity indices at the population level depending on population range (native vs. invasive).

Table S1: Gorse traits coefficient of variation (CV) within each population in the reference treatment (AT × Wet).

Table S2: Mean values for gorse traits from each country and population range (native or invasive).

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Conflict of interest statement. The authors declare that they have no conflict of interest.

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