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# Phenotypic variation along urban-to-rural gradients: an attempt to disentangle the mechanisms at play using the alien species *Matricaria discoidea* (Asteraceae)

**Charly Géron · Jonas J. Lembrechts · Rafiq Hamdi · Julie Berckmans · Ivan Nijs · Arnaud Monty**

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**Abstract** Cities often exhibit higher temperatures, drier soils and greater habitat fragmentation than rural areas, and may thus represent constraining growing environments for plants. This variety of environmental conditions along urban-to-rural gradients might lead to plasticity in plant traits. Urban conditions could affect plant traits such as germination or flower number — key variables for organismal fitness. These proxies of fitness could then potentially experience strong selection in urban environments. Trait variations among individuals are not only due to genotype or the environmental conditions: they can also result from the conditions in which the mother individual developed, i.e. environmental maternal effects. Understanding the impact of city environments on phenotypes might be especially important for alien plant species, as these are often showing exceptionally high density and diversity in cities. However, studies of the sources of alien plant trait variations in urban environments are rare. We conducted a simulated reciprocal common garden experiment using seeds of populations of *M. discoidea* along urbanization gradients in Belgium. These seeds were sown in growth chambers to study how germination, growth, and flowering traits of the alien species *Matricaria discoidea* vary in response to temperature (rural or urban) and soil (rural or urban) treatments and the urbanity (percentage of impervious surfaces) of its source population. We found predominant effects of seed mass and germination delay which materialized important

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C. Géron (✉) · A. Monty
Biodiversity and Landscape, TERRA Research Centre,
Gembloux Agro-Bio Tech, University of Liège,
5030 Gembloux, Belgium
e-mail: charly.geron@gmail.com

A. Monty
e-mail: arnaud.monty@uliege.be

C. Géron · J. J. Lembrechts · I. Nijs
Plants and Ecosystems, University of Antwerp,
2610 Wilrijk, Belgium
e-mail: jonas.lembrechts@uantwerpen.be

I. Nijs
e-mail: ivan.nijs@uantwerpen.be

R. Hamdi
Department of Physics and Astronomy, University
of Ghent, 9000 Ghent, Belgium
e-mail: rafiq.hamdi@meteo.be

R. Hamdi
Royal Meteorological Institute, 1180 Brussels, Belgium

J. Berckmans
Climawise, Solvynsstraat 37, 2018 Antwerp, Belgium
e-mail: julie.berckmans@gmail.com

environmental maternal effects. We observed a higher germination success and delay for heavier seeds, and a greater number of capitula and dry biomass for plants that germinated earlier. Climate and soil treatments led to plasticity in the majority of the measured traits, with a faster germination and heavier plants in the urban temperature treatment but lighter plants in the urban soil treatment. Our results therefore support the existence of predominant environmental maternal effects and phenotypic plasticity in response to temperature and soil treatments, but no visible evidence of local adaptation.

**Keywords** Urbanization · Alien plants · Environmental maternal effects · Simulated reciprocal garden · Local adaptation

## Introduction

The transformation of former rural zones into urban areas affects many parts of the world (Gross 2016; Hulme 2009). Europe is among the most urbanized continents and the rate of urbanization has reached unprecedented levels there, with an increase in urbanized areas of over 5% between 2000 and 2020 (Kuang et al. 2021). Urban areas consist of a complex assemblage of different human-related land covers (Ward et al. 2016), and this patchwork of microhabitats often supports a high plant diversity but isolated plant populations due to the habitat fragmentation (Gorton et al. 2020; Ortega and Pearson 2005; Schmidt et al. 2014). Urbanization also promotes the loss of native plant species and their replacement by alien species (McKinney 2006).

Because of their effects on environmental processes, urban environments represent particular growing conditions that are likely to be more stressful for plant populations than those found in the countryside (Alberti et al. 2003; Rosenzweig et al. 2018). Cities are well known for their modified microclimate and notably higher temperatures than the rural surroundings (urban heat island (UHI) effects (Oke 1981; Theeuwes et al. 2017)). These UHI effects are scale-dependent, and most apparent at the kilometer scale (Ren et al. 2013). The intensity of UHI effects positively correlates with the percentage of impervious surfaces (hereafter termed “urbanity”), and thus increases in highly urbanized areas (Oke 1981; Ward et al. 2016). Additionally, urban soils are often compacted and contain anthropogenic materials. These soil characteristics, combined with the high density of impervious surfaces, makes urban soils drier than rural ones (Fortuniak et al. 2006; Hamdi et al. 2020; Schmidt et al. 2014).

Plant trait variation can be expected along the urban-to-rural gradient due to several mechanisms (Géron et al. 2021; Nicotra et al. 2010). Phenotypic plasticity, *i.e.* the capacity of a genotype to change its phenotypes in response to heterogeneous conditions (Des Marais et al. 2013; Nicotra et al. 2010) may be an important strategy for species growing in cities as these environments represent highly variable growing conditions (Borowy and Swan 2020). Moreover, key traits for organismal fitness can be under strong selection pressure from environmental conditions (Gorton et al. 2020; Rivkin et al. 2019), so urban conditions may exert selection pressures that can cause adaptive divergence among populations along the urban-to-rural gradient—which can be defined as local adaptations (Donihue and Lambert 2015; Lourenço et al. 2017). When brought to new environmental conditions, plastic responses in reproduction traits for example can result in higher fitness, which are described as adaptive plasticity (Brachi et al. 2013; Brooker et al. 2022). Interestingly, when plasticity leads to optimal fitness, selection is weakest (Diamond and Martin 2021). The genetic structure of plant populations is not only dependent on selection processes and can also be the result of genetic drift—the random fluctuation of allele frequencies—which is increased for isolated and small populations such as in urban areas (Hagenblad et al. 2015; Lamarque et al. 2015; Santangelo et al. 2018).

The phenotypic response of an individual is not only due to its genotype and the environmental conditions it experiences: it can also be the result of the conditions in which the mother individual developed. Those environmental maternal effects can mediate success across generations (Mousseau and Fox 1998). Specifically, environmental maternal effects correspond to the influences of the maternal phenotype on the phenotype of its offspring, via mechanisms exclusive of any genetic information (Roach and Wulff 1987). For plants, environmental maternal effects are typically mediated by seed size or seed mass, with a possible positive relationship between seed size and the germination success and speed, and seedling development (Baskin and Baskin 1998).

Studies disentangling the sources of trait divergence between urban and rural plant populations are scarce, but some have already found differences in fitness-related traits between native plant populations depending on their habitat along the urban-to-rural gradients (Borowy and Swan 2020). For example, reduced dispersal abilities for urban populations of *Crepis sancta* compared to rural populations have been imputed to rapid evolution caused by a high dispersal cost in cities (Cheptou et al. 2008; and see: Gorton et al. 2018 on flowering time; Thompson et al. 2016 on cyanogenesis). Alien plant species can be useful for the understanding of evolutionary processes, as only a subset of the species gene pool is present in the invaded range, possibly resulting in higher genetic differentiation between populations than for native species (Hagenblad et al. 2015). Furthermore, some studies have shown the importance of high phenotypic plasticity or rapid evolutionary responses for alien plant species in their invaded ranges (Buswell et al. 2011; Dlugosch and Parker 2008; Parker et al. 2003). Additionally, alien plant species are useful in the description of rapid evolutionary responses, because their time since introduction is often known (Hagenblad et al. 2015). To our knowledge, studies disentangling the differences between alien plant species populations originating from various location along the urban-to-rural gradient are rare (but see for example Santangelo et al. 2018 and Thompson et al. 2016). Nevertheless, they are critically important for understanding how urban environments can impact plant species now and in the future.

Here, we studied the sources — i.e. phenotypic plasticity, local adaptation and environmental maternal effects—of germination, growth, and flowering trait variations of the model alien plant species *Matricaria discoidea* DC. (Asteraceae) in response to temperature (rural or urban) and soil (rural or urban) treatments and the urbanity of the populations (percentage of impervious surfaces) in its invaded range in Belgium. To do so, we performed a simulated reciprocal common garden experiment, under controlled conditions. We hypothesize that if local adaptation exists, *M. discoidea* plants from areas with higher urbanity values would perform better in urban conditions (temperature and/or soil) than plants from environments with lower urbanity values, and vice versa. We also hypothesize that, due to the associated stress, plasticity will be visible in individuals with a lower development in urban temperature and soil treatments, and that environmental maternal effects will have an important influence especially on early life stages.

## Methods

### Model species

*Matricaria discoidea* is a 4–40 cm tall, annual herbaceous plant, belonging to the Asteraceae family and native to North America (FNA 2006; POWO 2020; Roskov et al. 2000). It is heliophilic, mainly insect-pollinated but can self-pollinate and its dispersal syndrome is mainly barochoric (Bond et al. 2007). *M. discoidea* was first recorded in Belgium in 1893, probably in peri-urban agricultural areas and is now a widely naturalized alien species (Verloove 2021a, b). It is cosmopolitan and found in a large variety of habitats in Belgium, from man-made to more natural and agricultural ones (Verloove 2021a, b). We chose *M. discoidea* because it is widely present and abundant both in urban and rural areas in Belgium, has had sufficient time to undergo selection, and – being a small annual – allows easy experimental manipulation.

### M. discoidea populations and field sampling

We chose the Atlantic biogeographical region of Belgium (European Environment Agency 2011), i.e. the area north of the Meuse river, as study area, in order to limit variation in background climate (Géron et al. 2021). This region has a temperate oceanic climate, with relatively cool and wet summers, and mild and humid winters (Royal meteorological institute (RMI) 2021). It encompasses Flanders, Brussels Capital Region, and the north of Wallonia, and contains some of the most urbanized parts of Belgium (average urbanity in Flanders, for example, equaled 16% in 2015, De Ridder et al. 2015a, b, Supplementary material 1, Fig. 1) but also rural zones.

We selected 18 populations of *M. discoidea* using remotely sensed urbanity ((European Environment Agency 2019), percentage of impervious surfaces, original scale: 400 $m^2$) at a scale of 1 $km^2$. This scale corresponds to the one at which UHI effects mostly operate (Brans et al. 2017; Kaiser et al. 2016). Populations were harvested in 1 $km^2$ resolution areas with urbanity values ranging from 0.8 to 81.8%, and were at least 5 km apart (Supplementary Material 1). Studies conducted in the same geographical area as ours, such as Brans et al. (2017) and Kaiser et al. (2016), considered 1 km$^2$ resolution areas with urbanity values of at least 16% as urbanized. ArcMap 10.5.1 (ArcGis Desktop, 2017) was used for spatial processing. In June 2018, the seeds from 10 randomly chosen individuals from each population were collected. Individuals with obvious damages or that had been cut or mown were excluded.

## Experimental design

We grew the seeds of the *M. discoidea* populations in a reciprocal common garden design under controlled conditions, fully crossing the 18 populations with the reproduced temperature (urban or rural) and soil (urban or rural) treatments in two identical growth chambers, whilst maintaining the same precipitation, light and humidity. A total of 648 individuals were studied: 18 populations × 10 mother plants × 2 climate treatments × 2 soil treatments = 720, with four populations with fewer individuals as no seeds could be collected from some of their mother plants.

Temperature treatment: to build the temperature treatment, we used gridded modelled hourly surface temperature data (~0 cm) for the region of Brussels (Berckmans et al. 2018, containing the city center as well as the rural countryside) at a resolution of 1 km$^2$. Within the period 2000–2010 for which these surface temperature data were available, the year 2004 had conditions closest to the 1981–2010 climatic means so its weather pattern could be seen as the most representative for the 30-year period (Royal meteorological institute (RMI) 2021). Consequently, we chose the temperature data corresponding to the period April to September 2004 (extent of 900 km$^2$ centered on Brussels, validated with observations from weather stations in Brussels Capital Region, Berckmans et al. 2018). Additionally, the temperature contrast between the urban and rural areas of the region of Brussels is comparable to the one observed at the scale of the entire study area (De Ridder et al. 2015a). To select urban and rural weather locations representative of the urbanity of the populations that we harvested, we calculated the mean urbanity for the five populations with the highest urbanity and for the five populations with the lowest urbanity (54 and 1.2%, respectively; considering the urbanity values of all populations would have diluted the differences in urbanity and thus reduce the contrast in temperature). Then, we randomly selected ten 1 km$^2$ pixels with an urbanity close to 54% within the region around Brussels (corresponding to the 900 km$^2$ temperature data extent) and considered them as urban weather locations. We selected ten 1 km$^2$ areas with an urbanity close to 1.2% within the same region as rural weather locations. For each week of the April–September period, we calculated the weekly mean minimum and maximum surface temperatures over these urban and rural weather locations.

Temperature programs for the growth chambers were built for one day as: the weekly mean minimum surface temperature as the night temperature (plateau from 23h00 to 2h00) and the weekly mean maximum surface temperature as the mid-day temperature (plateau from 11h00 to 14h00). The temperature variations between these two plateaus were simplified by continuous increases or decreases. These daily temperature programs were repeated during seven days, in order to form weekly temperature programs for each of the 25 weeks spanning the April-September period. Mean temperature over the experiment period was 15.3 °C for the rural temperature program, and 16.8 °C for the urban temperature program (Supplementary Material 2).

Two fitotron® SGC 120 growth chambers (Weiss Technik UK, Loughborough) were used: one with the urban temperature program and one with the rural temperature program. We applied the same light treatment in both, reproducing the weekly variations of night and day length for Brussels based on www.timeanddate.com/sun aligned with the sunrise and sunset times (12 × 36 W fluorescent lamps, set at the maximum intensity of ~ 620 µmol photons m$^{-2}$ s$^{-1}$ at the top of the canopy, mean day length of 15 h over the experimental period, Supplementary Material 2). We also applied the same watering treatment, calculated weekly for the period of the experiment. This watering treatment was based on modelled precipitation data for 2004 in Brussels (initial scale of 16 km$^2$, simulated rainfall of 447 mm over the experimental period, see Supplementary material 2, Berckmans et al. 2018). Likewise, the same relative humidity percentage was set in both chambers. This relative humidity percentage was calculated based on the weekly climatic means for Uccle, Belgium, for the period 1981–2010 (mean relative humidity of 75% over the experimental period, Supplementary Material 2, Royal meteorological institute (RMI) 2021).

Soil treatment: Five 1 kg soil samples from five locations near one of the urban populations and five 1 kg soil samples from five locations near one of the rural populations were collected. Urban soil samples were mixed together to create a composite urban soil, hereafter called urban soil treatment. The same was done for rural soils to create the rural soil treatment. Both urban and rural soil treatments were analyzed for their nutrient content, texture and pH (Supplementary Material 3, Tinlot provincial laboratory, Belgium) and cultivated for one month in a greenhouse prior to the experiment, at constant moisture, 12 h light, and 25 °C. All seedlings that germinated during that month were removed to reduce weed contamination during the experiment. Urban soil was more calcareous, had lower nutrient content and was more drained, and contained a higher proportion of clay particles but less humus than the rural soil (Supplementary material 3).

*M. discoidea* plants were cultivated in the urban and rural temperature growth chambers with either the urban or rural soil in falcon tubes (11.5 cm deep, 50 ml volume), as these plants have a small stature and root system (Supplementary material 1 Fig. 1, Supplementary material 4). The tubes were pierced at the bottom to allow good drainage (2 holes with a diameter of 5 mm each). A total of 648 falcon tubes were used: 18 populations × 10 mother plants × 2 temperature treatments × 2 soil treatments = 720, with two urban and two rural populations with fewer tubes as no seeds could be collected from some of their mother plants. The 324 falcon tubes in each growth chamber were placed on a single shelf to avoid mutual shading. Every two weeks, the temperature treatments and the associated falcon tubes were switched between the two chambers to avoid any bias related to the growth chambers.

## Launch and follow up of the experiment

The seeds harvested in the field were visually sorted using a binocular magnifier to remove any damaged ones and weighed to the nearest 0.01 mg (Mettler Toledo analytical scale AG204, USA). Then, two seeds from each individual of each population were randomly selected and sown in each treatment combination (Supplementary Material 4). Soils were made damp prior to sowing.

Germinations were counted every other day from the day of sowing until no more germination was noticed during a period of 14 days. When the two seeds in a pot both germinated, only the first to germinate was kept. The germination delay was taken for each pot as the difference in number of days between the day of sowing and the day when that first seed germinated (minimum = 7 days, maximum = 112 days).

The experiment was stopped after 25 weeks, when most of the plants were senescent and 45% of the plants had died. Then, the number of produced capitula per plant was counted. Finally, we harvested the aboveground biomass, dried it for 72 h at 60 °C and weighed it.

Germination success and number of capitula provide information on reproduction and are usually considered as proxies of the fitness of the plants. Traits considered as proxies of plant fitness can be used to detect local adaptation, as they can be subject to selection (Lortie et al. 2021). Traits such as the germination delay and dry aboveground biomass cannot be directly linked to the fitness of the plants, yet can still be genetically controlled. They can give information on the plastic response of the plants to the conditions (Childs et al. 2010; Gremer et al. 2016; Kawecki and Ebert 2004; Rühl et al. 2016).

## Statistical analyses

### *Seed mass*

The relationship between seed mass and the urbanity of plant populations was analyzed using linear mixed models, as the seed mass was normally distributed (Shapiro-Wilkinson normality test: $p > 0.05$). The addition of the population and mother plant identities as a nested random intercept increased the fit of the model (Akaike Information Criterion (AIC) decreased with more than two units, Galwey 2006).

### *Developmental traits*

The relationships between the response variables—germination (success and delay) and development (capitulum number and dry aboveground biomass)—and the explanatory variables population urbanity (continuous), soil and temperature treatment (categorical), and either the seed mass or germination delay (continuous), were analyzed using generalized or linear mixed models (R package lme4, Bates et al. 2020). We included one variable accounting for environmental maternal effects (either seed mass or germination delay) for each of the models to acknowledge that environmental maternal effects can be accounted for through different variables such as seed mass or germination timing (Bischoff et al. 2010). The choice of the environmental maternal effect variable was made by comparing the AIC of models containing either seed mass or germination delay, keeping the variable that led to the lowest AIC (the difference in AIC was at least two units or more for each of the response variable). Consequently, we analyzed germination success and delay with the seed mass, and capitulum number and dry aboveground biomass with the germination delay. The addition of population and mother plant identity as a nested random intercept increased the fit of the mixed models for each of the response variables (AIC decreased with more than two units, Galwey 2006). Therefore, this nested random intercept was included in the model for each response variable. Germination success was modelled with a binomial distribution, and germination delay, capitulum number with a Poisson distribution (see model structure in Supplementary material 5, Crawley 2013). We detected zero inflation for the generalized linear models of the capitulum number (DHARMa residuals diagnostic, R package DHARMa, Hartig and Lohse 2020), which we corrected using zero-inflated generalized linear mixed models with a Poisson distribution (R package glmmTMB, Brooks and Brien 2021). Dry aboveground biomass was normally distributed (Shapiro-Wilkinson normality test: $p > 0.05$) and was analyzed with linear mixed models.

For each of the response variables, the model included two-way interactions of the temperature treatment, soil treatment and urbanity of the populations to test for plasticity and local adaptation. For each of the models, we calculated the pseudo-R-squared (R package MuMIn, K. Barton 2009).

All statistical analyses were performed in R, version 3.5.2 (R Core Team 2018), and $p = 0.05$ was taken as threshold for significance.

## Results

### Seed mass

The average mass of the seeds of *M. discoidea* harvested at the locations of the populations was not influenced by the urbanity of the populations ($p = 0.63$, Supplementary material 6, Fig. 1).

**Fig. 1** Reaction norms for the soil (**A**, **C**, **E**, **G**) and temperature treatments (**B**, **D**, **F**, **H**) for the germination success (**A**, **B**), germination delay (**C**, **D**), capitulum number (**E**, **F**) and aboveground dry biomass (**G**, **H**). The 18 populations are colored by their urbanity. 95% confidence intervals are represented for each of the populations by the error bars. Note that the y-axes do not have the same scale for each response variable to improve visual interpretation ▸

### Life history traits

Germination success and delay, number of capitula and the dry aboveground biomass, depended on at least either the soil treatment, temperature treatment or the seed mass or germination delay variables. They did not depend on the urbanity of the populations, except for the germination delay, which depended on the two-way interaction between the soil and temperature treatments and the urbanity of the populations. This hints to the complexity of factors influencing the life history traits variations of *M. discoidea*.

Germination success varied with soil type and seed mass (Table 1), leading to higher germination success for heavier seeds, and in the urban soil treatment (germination success 140% higher in the urban soil than in the rural soil treatment, Fig. 1 A, B).

The germination delay varied as a function of all explanatory variables and the two-way interactions between the temperature and soil treatments and the urbanity of the populations (Table 1). This resulted in later germination for heavier seeds, but 2% and 8% earlier germination in the urban soil and the urban temperature treatment, respectively (Fig. 1 C, D). Additionally, plants from areas with high urbanity germinated later in the urban soil and in the urban temperature treatment (Table 1).

The number of capitula was only affected by the germination delay (Table 1), which led to the production of a lower number of capitula for plants that germinated later (Fig. 1 E, F).

The dry aboveground biomass was influenced by the temperature and soil treatments and the germination delay. We observed 27% heavier plants in the urban temperature treatment but 5% lighter plants in the urban soil treatment (Table 1, Fig. 1 G, H). Additionally, plants that germinated later had a lower aboveground biomass (Table 1).

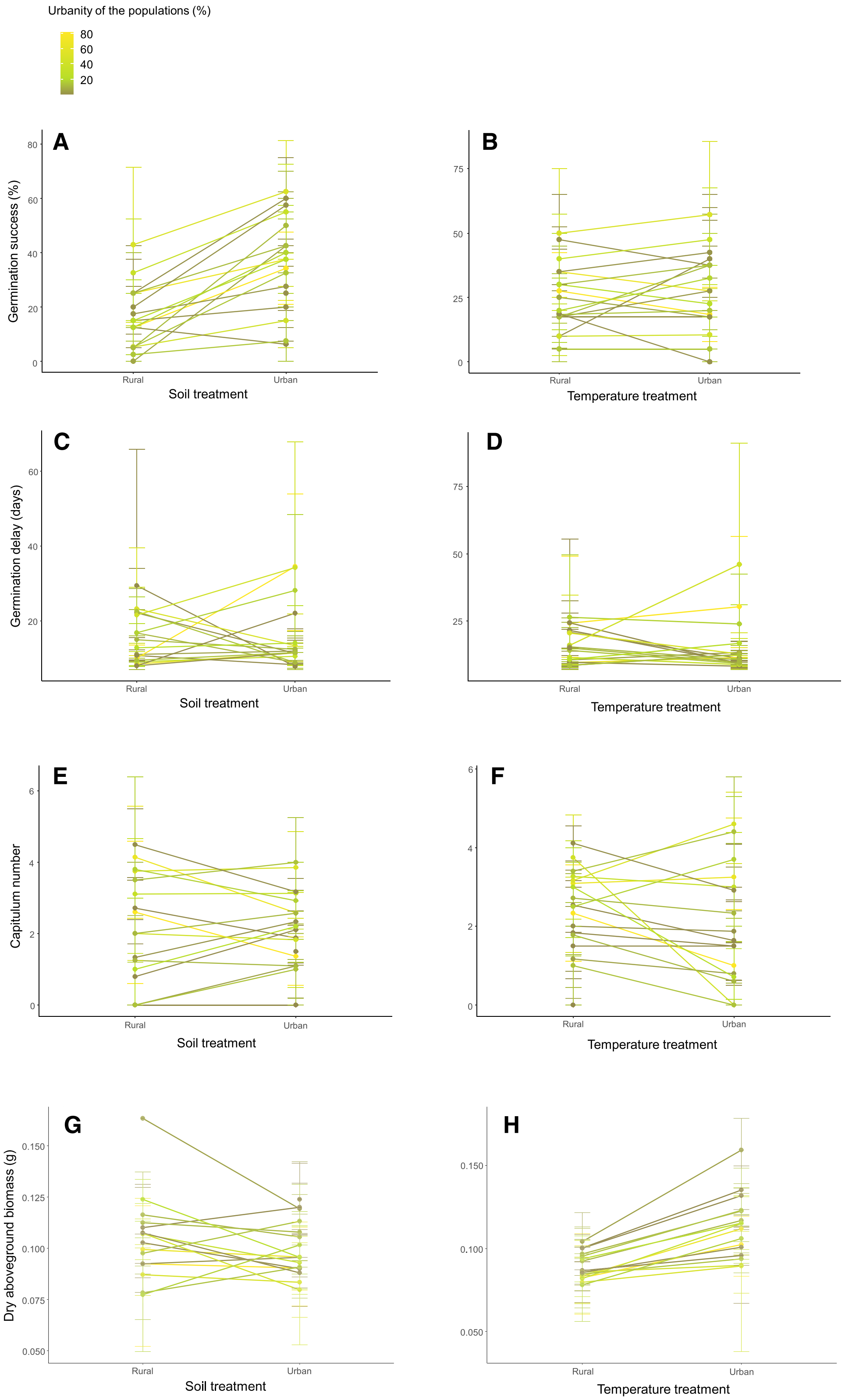
Urbanity of the populations (%)
80
60
40
20
A
Germination success (%)
0
20
40
60
80
Rural
Urban
Soil treatment
B
0
25
50
75
Rural
Urban
Temperature treatment
C
Germination delay (days)
20
40
60
Rural
Urban
Soil treatment
D
25
50
75
Rural
Urban
Temperature treatment
E
Capitulum number
0
2
4
6
Rural
Urban
Soil treatment
F
0
2
4
6
Rural
Urban
Temperature treatment
G
Dry aboveground biomass (g)
0.050
0.075
0.100
0.125
0.150
Rural
Urban
Soil treatment
H
0.050
0.100
0.150
Rural
Urban
Temperature treatment

**Table 1** Estimates, standard errors (between brackets) and model parameters for the models testing for the drivers of the germination success, germination delay, capitulum number and dry aboveground biomass of *M. discoidea*

| | Germination success | Germination delay | Capitulum number | Dry aboveground biomass |
|---|---|---|---|---|
| (Intercept) | **– 3.51$^{***}$ (0.43)** | **2.15$^{***}$ (0.15)** | **1.61$^{***}$ (0.19)** | **0.11$^{***}$ (< 0.01)** |
| Temperature urban | 0.12 (0.28) | **– 0.53$^{***}$ (0.08)** | 0.33 (0.21) | **0.02$^{**}$ (< 0.01)** |
| Soil urban | **1.48$^{***}$ (0.27)** | **– 0.37$^{***}$ (0.07)** | – 0.09 (0.17) | **– 0.02$^{*}$ (< 0.01)** |
| Urbanity | 0.01 (0.01) | < – 0.01 (< 0.01) | < 0.01 (< 0.01) | < – 0.01 (< 0.01) |
| Temperature urban × Urbanity | – 0.01 (0.01) | **< 0.01$^{*}$ (< 0.01)** | < – 0.01 (< 0.01) | < – 0.01 (< 0.01) |
| Temperature urban × Soil urban | 0.35 (0.30) | **0.37$^{***}$ (0.09)** | – 0.34 (0.20) | 0.01 (0.01) |
| Soil urban × Urbanity | < – 0.01 (0.01) | **0.01$^{***}$ (< 0.01)** | < – 0.01 (< 0.01) | < 0.001 (< 0.001) |
| Seed mass | **6.08$^{***}$ (1.53)** | **3.43$^{***}$ (0.49)** | NA | NA |
| Germination delay | NA | NA | **– 0.04$^{***}$ (< 0.01)** | **< – 0.01$^{***}$ (< 0.01)** |
| AIC | 1114.50 | 2206.02 | 935.00 | – 900.80 |
| BIC | 1159.20 | 2241.44 | 973.9 | – 863.37 |
| Log likelihood | – 547.25 | – 1093.01 | – 456.50 | 473.66 |
| Num. observation | 648 | 255 | 254 | 222 |
| Num. groups: Individuals: Population | 168 | 131 | 131 | 118 |
| Num. groups: Population | 18 | 18 | 18 | 17 |
| Var: Individuals: Population (Intercept) | 0.78 | 0.27 | < 0.01 | < 0.01 |
| Var: Population (Intercept) | 0.35 | 0.05 | < 0.01 | < 0.01 |
| $R^2$ fixed | 0.21 | 0.18 | 0.60 | 0.27 |
| $R^2$ random | 0.32 | 0.65 | 0.13 | 0.23 |

For each of the response variables, the model includes the population and mother plant identity as a nested random intercept (see Methods). This nested random intercept was significant and included in the model for each response variable. Significant effects are in bold, and coded as follows: $*** = p < 0.001$; $** = p < 0.01$; $* = p < 0.05$. NAs indicate covariates not present in the model. That is to say, models for the germination success and the germination delay contained seed mass covariate, and models for the capitulum number and dry aboveground biomass contained the germination delay covariate, respectively (see methods). The "random" pseudo-$R^2$ corresponds to the variance explained by the entire mixed model whereas the "fixed" pseudo-$R^2$ corresponds to the variance explained by the fixed effects only

### Urbanity of the populations

The urbanity of the populations had a very limited effect on life history traits of *M. discoidea*, as it only explained the variation in germination delay, and only in interaction with the soil and temperature treatments (Table 1). Plants from areas with higher urbanity and grown in urban soil or urban temperature treatments germinated later (Table 1).

## Discussion

We studied the sources of variation in germination, growth, and number of capitula of *M. discoidea* in response to urban or rural temperature and soil treatments, and its population urbanity. The strong influence of either the seed mass or germination delay on all the life history traits we measured, suggests predominant environmental maternal effects with decreased development and fitness of lighter seeds and plants that germinated later (Donohue 2009). We observed plasticity in most of the measured traits with an overall negative effect of the urban temperature and soil treatments on most of them, except for the aboveground biomass. Importantly, the effects of the temperature and soil treatments, seed mass and germination delay variables, and their interactions, on life history traits variations seem to imply that the trait expression for *M. discoidea* is a complex interplay of phenotypic plasticity and environmental maternal effects.

The high importance of the seed mass and the germination delay variables emphasizes the need to account for environmental maternal effects in studies of urbanization effects on plants (Baskin and Baskin 1998; Nicotra et al. 2010). Heavier seeds were found to have a higher germination success, which is in line with the literature (Byers et al. 1997). The germination delay had a strong negative effect on individual's performance, with decreased fitness in plants that germinated later. Indeed, changes in germination patterns such as its timing, have been found to influence population performance more than changes in any other life stage (Donohue 2009). This also reinforces the importance of using additional variables than seed mass to account for environmental maternal effects when looking at later stages of the plant life. Environmental maternal effects are often overlooked and considered to play a minor role in the later stages of plant life, such as reproduction or survival (Bischoff et al. 2010). As environmental maternal effects seem to play an important role in life history traits variations of *M. discoidea,* it is crucial to use seeds of populations that have been harvested in a relatively short period of time to avoid bias due to differences in growing conditions between populations. This is especially true for annual species because individuals mainly germinate in autumn or spring (Bond et al. 2007). The period during which plants develop and reproduce affects the maturation of the seeds. Furthermore, the maturation of the seeds influences the amount of reserves they contain, which has an impact on their germination. For example, germination success is higher for spring-matured versus autumn-matured individuals in other annual species (Gutterman 2009). We have minimized the impacts of this factor in our study as seeds from all the populations were harvested in early summer, and consequently corresponded to only one maturation period.

Previous studies showed plasticity of plant traits to city environments such as urban temperature or soil conditions, but with results contrasting with ours. For example, we noted a higher germination success, a faster germination and lower dry aboveground biomass in the urban than in the rural soil treatment. On the contrary, Borowy and Swan (2020) found a decreased germination success and an increased biomass in urban soil conditions. In our case, the faster germination we observed in urban soil might be due to its higher drainage, a factor found to increase germination speed and success (Benvenuti 2003; Sladonja et al. 2014). We found that plants had a longer germination delay and a higher dry aboveground biomass in the urban temperature treatment especially for plants from more rural environments. Contrasting results have been found in urban conditions regarding the timing of plant development for different species. While Gorton et al., (2018) found later flowering of *Ambrosia artemisiifolia* in urban sites, Franks et al., (2007) detected earlier flowering events of *Brassica rapa* in (drier) urban conditions.

In our study, we did not find signs of local adaptation of populations of *M. discoidea* from areas with high urbanity values to urban conditions, or of populations from areas with low urbanity values to rural conditions. Additionally, we did not find overall positive reaction norms, with populations from high urbanity environments showing higher trait values in urban treatment conditions, which would indicate that we have not found signs of adaptive plasticity either (Diamond and Martin 2021). Some recent studies have proven the existence of local adaptations to cities, such as a lower resistance to freezing events for urban population of *Trifolium repens* in Canada; when others found no signature of local adaptation to urban environments for example in the case of *Taraxacum officinale* in Belgium (Pisman et al. 2020; Thompson et al. 2016). It is possible that we would have found more signs of local adaptations if the environmental maternal effects would have been smaller. Environmental maternal effects are decreased for the seeds produced by the organisms that are experiencing the same growing conditions (Rossiter 1996). Reducing the environmental maternal effects can thus be done using the first generation of individuals grown under common conditions instead of studying individuals derived from seeds produced in the populations' habitat (Monty et al. 2009). Environmental maternal effects have been shown to be important in the evolution of plant species. For example, Galloway (2005) found that they influenced the germination timing of *Campanula americana,* and impacted its adaptation to the local light conditions. However, we here did not test the influence of environmental maternal effects on the fitness of *M. discoidea* populations in interaction with their urbanity. Therefore, drawing conclusions about potential effects of environmental maternal effects on the selection of *M. discoidea* along urban-to-rural gradients is beyond the scope of our study. Finally, in order to thoroughly detect local adaptations, future experiments should make detailed measurements of fitness on individuals from seed to seed production, and if possible perform studies over multiple generations which can however represent technical challenges (Lortie et al. 2021).

Disentangling the sources of trait variations is complicated, and our study has several limitations. The soil treatment we used may not be representative of the wide range of soil conditions that can be encountered in both rural and urban environments. Alternatively, one could consider the use of several urban and rural soils instead, but such additional complexity of the soil treatment could further complicate the results. In our study, we took into account the habitat of spatially defined populations, using the percentage of impervious surfaces in their vicinity as a proxy of their urbanity. Even if the extremities of the urbanization gradient were well represented in our dataset, it is possible that intermediate situations were lacking in our population selection. Additionally, the analyses we conducted consider the urbanization gradient but prohibit us from accounting for possible differences in developmental and fitness traits among the populations (Gorton et al. 2020). While local adaptation was not detected for populations of *M. discoidea* with respect to flowering traits, other patterns could exist on other, unmeasured, traits such as the characteristics of the produced seeds. Additionally, detection of local adaptation to cities in alien plant species would require the study of more model species or experiments over multiple generations (Anderson et al. 2012; Franks et al. 2007; Monty et al. 2013). Alien plant species are present in a greater concentration in urban environments, and for some of them it has been possible to track their invasion process (McKinney 2006). In our case, *M. discoidea* has been present for about 100 years in Belgium, yet we did not detect differences between populations from areas with higher or lower urbanity values. Therefore, our study using an alien plant species is not in line with some other studies on native organisms that found that urbanization can lead to their rapid evolution (Brans et al. 2017; Shochat et al. 2006). A possible explanation could be that this species was first noticed in peri-urban environments about a century ago, and that it has co-evolved with the progression of urbanization to the present day, resulting in no differences between populations located in rural or urban areas (F. Verloove 2021a, b). Consequently, more studies using alien plant species are needed in order to investigate possible rapid plant adaptations to urban conditions as cities experience harsher and more significant effects of global changes (Bader et al. 2018; Brans et al. 2017; Shochat et al. 2006). Nonetheless, our study should be seen as part of the growing literature body providing a better understanding of how urban environments impact plant species.

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**Declarations**

**Competing interests** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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