The complexity underlying invasiveness precludes the identification of invasive traits: A comparative study of invasive and non-invasive heterocarpic Atriplex congeners

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Abstract

Heterocarpy enables species to effectively spread under unfavourable conditions by producing two or more types of fruit differing in ecological characteristics. Although it is frequent in annuals occupying disturbed habitats that are vulnerable to invasion, there is still a lack of congeneric studies addressing the importance of heterocarpy for species invasion success. We compared two pairs of heterocarpic Atriplex species, each of them comprising one invasive and one non-invasive non-native congener. In two common garden experiments, we (i) simulated the influence of different levels of nutrients and population density on plants grown from different types of fruits and examined several traits that are generally positively associated with invasion success, and (ii) grew plants in a replacement series experiment to evaluate resource partitioning between them and to compare their competitive ability. We found that specific functional traits or competitiveness of species cannot explain the invasiveness of Atriplex species, indicating that species invasiveness involves more complex interactions of traits that are important only in certain ecological contexts, i.e. in specific environmental conditions and only some habitats. Interestingly, species trait differences related to invasion success were found between plants growing from the ecologically most contrasting fruit types. We suggest that fruit types differing in ecological behaviour may be essential in the process of invasion or in the general spreading of heterocarpic species, as they either the maximize population growth (type C fruit) or enhance the chance of survival of new populations (type A fruit). Congeners offer the best available methodical framework for comparing traits among phylogenetically closely related invasive and non-invasive species. However, as indicated by our results, this approach is unlikely to reveal invasive traits because of the complexity underlying invasiveness.
Introduction

The identification of species traits that promote invasiveness has for decades been one of the main challenges in invasion ecology [1–3]. This question is of great significance for the understanding of plant success in general and particularly the mechanisms of plant invasions [4,5]. It has been documented that invasive plant species, compared to their non-invasive congeners, generally attain greater values of life-history and functional traits, such as plant size, fecundity, growth rate, specific leaf area, photosynthetic capacity or survival (see [4,6] and references therein). However, contradictory results of global analyses searching for important traits such as plant size [4,7], seed mass [8,9] and plant fecundity [8,10] have been reported, confirming that it might be impossible to predict invasibility based on traits alone [9,11].

Another frequently addressed question is whether invasive species possess higher phenotypic plasticity than co-occurring natives [10,12,13]. Invasive plant species have repeatedly been shown to be more phenotypically plastic in a wide range of traits correlated with resource supply management [10,13–15], but most studies have failed to find an associated fitness benefit [13,16]. With respect to the vague results of the trait-based approach to predicting invasive potential, some authors have stated that the predictive power of traits is weak [11,17,18]. Species invasiveness clearly involves more complex interactions of traits that may be important only in certain ecological contexts. Therefore, one of the more targeted approaches how to improving the current knowledge about traits determining biological invasions is to perform more intensive studies on particular model systems of organisms [17].

The fluctuating resource hypothesis, postulated by Davis, Grime and Thompson [19], states that invasions are facilitated by high resource availability resulting from environmental disturbances. The hypothesis assumes that invading species are more successful in invaded communities, provided that they do not face intense competition for resources from resident species. Anthropogenic habitats characterized by higher availability of resources and frequent disturbances are known to be the most invaded [20]. One of the strategies plants use to spread effectively despite frequent disturbances is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]). The production of different types of diaspores with differing dispersal potential (e.g. with or without a pappus) and patterns of dormancy is heterodiaspory (sensu [21,22]).
Atriplex species (A. sagittata and A. tatarica), which have their non-invasive and non-native congeners (A. hortensis and A. rosea, respectively), grow in Central Europe [44]. A. sagittata and A. hortensis belong to the section Atriplex [49], which represents primitive oraches within the genus Atriplex [50]. Whereas A. sagittata is the most invasive representative of the genus in Central Europe, A. hortensis is a species with limited distribution that is strongly dependent on its relatively common cultivation and subsequent escapes from cultivation [43]. The section Sclerocalymma contains A. tatarica and A. rosea [49], which are evolutionarily derived species within the genus Atriplex with C_{4} photosynthesis [50]. Atriplex tatarica is a common species distributed mainly in the lowlands of Central Europe and has been expanding further in recent years [51]. On the other hand, A. rosea is a species that used to be relatively common in Central European villages; today, however, it remains only at a few localities [44]. The section Atriplex comprises species bearing three types of fruit (i.e. A. sagittata–A. hortensis group) with different patterns of dormancy and germinability both among fruit types and between species [43]. By contrast, species of the section Sclerocalymma produce only two types of fruit (i.e. the A. tatarica–A. rosea group) that are not too different in the level of dormancy and germination characteristics both overall and between species [43].

In this study, we compared two pairs of phylogenetically closely related heterocarpic congeners, A. sagittata–A. hortensis and A. tatarica–A. rosea, in two common garden experiments, hypothesising that (a) different traits explaining invasiveness may exist between different evolutionary lineages and that (b) heterocarpy is an important trait positively related to invasiveness. To test these hypotheses we carried out two experiments comparing (i) plants grown from different types of fruits under different levels of nutrients and population densities, focusing on traits that are generally positively associated with invasion success; and (ii) the competitiveness of species pairs vying for the same resources. By studying two pairs of closely related heterocarpic species with different patterns of dormancy and germinability, we addressed the following questions: (1) Are there any differences in traits between invasive and non-invasive Atriplex species that are consistent across evolutionary lineages? (2) If so, are these differences dependent on nutrient supply and neighbour density? (3) Are there any differences in traits between plants originating from different fruit types? (4) Do trait differences between plants growing from different fruit types contribute to invasion success? and (5) Does competitive ability explain invasiveness across evolutionary lineages?

**Materials and methods**

**Ethics statement**

The collections used for this study did not involve protected species, and no specific permissions were required for sampling activities in these locations.

**Study system**

The genus Atriplex L. (family Amaranthaceae) comprises about 270 species, whose distribution centres are primarily deserts and semideserts of most continents [51]. Many of them are annuals that typically exhibit some kind of heterocarpy [21].

We compared two closely related invasive and non-invasive Atriplex species belonging to two different taxonomic groups (see Table 1 for a detailed overview of species characteristics). The groups differ especially in the number of heterocarpic fruits and the type of photosynthetic pathway. The more ancestral section Atriplex, represented by A. sagittata and A. hortensis, is characterized by three types of fruits and the C_{3} photosynthetic pathway. The evolutionarily more derived section Sclerocalymma includes the C_{4} species A. tatarica and A. rosea, which produce only two different types of fruit. The fruits differ both morphologically (mainly in
colour and the presence/absence of bracteoles) as well as ecologically: (1) The first fruit type (hereafter referred to as type A), present only in representatives of the section Atriplex, originates from female or bisexual ebracteate flowers. Fruits of this type are small, black and lens-shaped with a glossy, smooth testa and a 5-lobed perianth. (2) The second fruit type (type B) is produced by female bracteate flowers. It is intermediate in size and has a similar appearance to the previous type, but it is covered by extended bracteoles. (3) The third fruit type (type C), produced by female bracteate flowers, is rather large, brown and covered by extended bracteoles that are larger than those of type B fruits. The individual fruit types differ especially in their germinability rates and patterns of dormancy. While type A fruit is the most dormant and forms a persistent seed bank, type C fruit is non-dormant and ensures almost 100% germination in the first year after ripening. Type B fruits exhibit intermediate germination characteristics [43].

### General description of experiments

We compared two pairs of invasive and non-invasive species (Atriplex sagittata with A. hortensis and A. tatarica with A. rosea) in two common garden experiments. In the first experiment (hereafter referred to as the “heterocarpy experiment”), we compared species for several traits across different fertilization levels and population densities, and searched for trait differences among plants grown from different types of fruit. In the second experiment (hereafter referred to as the “replacement experiment”), we used the replacement series design to examine...
whether species belonging to the same group use the same resources to compete against each other and to compare their competitive ability.

Both experiments were conducted in an experimental garden at Průhonice in 2014, Central Bohemia, Czech Republic (49° 59’41” E, 14° 33’56” W). Fruits of all Atriplex species, i.e. *A. sagittata*, *A. hortensis*, *A. tatarica* and *A. rosea*, were collected in autumn 2013 in a waste ground in Prague, Czech Republic (50° 07’27” E, 14° 30’29” W). Bracts were removed from fruits, and fruits were sorted according to the species and type (A, B and C), and stored in paper bags at room temperature until use.

Seeds were sown into small plastic flats 7 cm (width) × 7 cm (length) × 9 cm (depth) and watered daily. Before sowing, all seeds were scarified (see [61]) to reach high germination percentages (see [43]). After 20 days, seedlings were transplanted into larger experimental pots 19 cm (width) × 19 cm (length) × 19 cm (depth) (6.9 L) in size. To reduce the variation in initial seedling size, only seedlings that germinated in the course of a single day (i.e. the day representing the peak of the population germination) were used for the experiments. Plants that died after being transplanted were replaced with ones of comparable size for the first two weeks of each study, after which no plants needed to be replaced.

**Heterocarpy experiment**

We used a randomized block design with 8 replicates. Each block consisted of 24 pots containing *A. sagittata* together with *A. hortensis* (representing a combination of two species, three fruit types, two densities and two fertilization levels) and 16 pots containing *A. tatarica* together with *A. rosea* (representing a combination of two species, two fruit types, two densities and two fertilization levels).

The experiment consisted of (1) a single plant in the pot (low density) and (2) one target plant surrounded by four border plants; the plants in each pot had a regular spatial distribution, with the target plant located in the centre and border plants in the space between the centre and the pot corners (high density). The fertilization treatment included (1) watering with a Cererit solution alternated with pure water (low fertilization), (2) watering only by the Cererit solution (high fertilization). The pots were watered every three days, and the same amount of water/fertilizing solution was used for each pot (0.2 L). Sterilized sand subsequently fertilized depending on the treatment was used as the potting substrate. For fertilization, the complete fertilizer Cererit was used (N—11%, P₂O₅—9%, K₂O—14%, MgO—1.5%, trace elements: B, Co, Cu, Mg, Mn, Zn).

We measured plant size (cm) four times per season (14 June, 30 June, 19 July and 25 August) to obtain a non-destructive estimate of the relative growth rate (RGR). The RGR was calculated as the linear-regression slope of ln(plant size). The experiment was run until all plants had matured and bore ripe fruits. This took 113 days, after which we dried and weighed each plant to determine fruit and stem mass (g).

**Replacement experiment**

For our inter-specific competition experiment, only non-dormant type C fruits were used because of their high germinability [43] and high rate of seedling survival [47]. The competition experiment was set up in the de Wit [62] replacement series design, i.e. whilst the overall density is held constant, frequencies of each of the two species grown together are varied from 0 to 100%. To determine the constant final yield of individual species, monocultures of 1, 2, 4, 6 and 8 plant(s) per pot were planted. All plant species reached constant final yield at 4 to 8 plants per pot (Kruskall-Wallis test; \( P \geq 0.262 \)). The final density used in the replacement series was 8. Six replications were used per density. Five different frequencies of two species
(i, j) were used: 0i:8j, 2i:6j, 4i:4j, 6i:2j, 8i:0j. Each mixture combination contained an invasive and non-invasive species of each phylogenetic group, i.e. A. sagittata—A. hortensis and A. tatarica—A. rosea. On the day the plants were harvested (after 119 days of the experiment), they were dried at 80˚C for 48 hours, and the total mass of all plants was weighed separately.

Relative yield (RY) and relative yield total (RYT) were calculated for each species according to the following formulae [63,64]:

relative yield of species $i$: $\text{RY}_i = \frac{Y_{ij}}{Y_{ii}}$

relative yield of species $j$: $\text{RY}_j = \frac{Y_{ji}}{Y_{jj}}$

relative yield total: $\text{RYT} = \text{RY}_i + \text{RY}_j$,

where $Y_{ij}$ or $Y_{ji}$ is the total yield of species $i$ (or $j$) when grown with species $j$ (or $i$), and $Y_{ii}$ (or $Y_{jj}$) is mean total yield of species $i$ (or $j$) in monoculture.

The gain or loss of biomass due to inter-specific competition was determined by calculating the aggressivity ($A$) of each species as follows [64]:

aggressivity of species $i$: $A_i = \frac{\text{RY}_i}{p} - \frac{\text{RY}_{ij}}{q}$

aggressivity of species $j$: $A_j = \frac{\text{RY}_j}{q} - \frac{\text{RY}_{ij}}{p}$

where $p$ and $q$ are proportions of species $i$ and $j$, respectively, in mixture ($p + q = 1$). An aggressive species will have a higher aggressivity index than a subordinate species [64,65].

Relative yields ($RY$) were then plotted into replacement diagrams against appropriate planting proportions. Comparisons of the actual $RY$ of each species with their expected $RY$ (the species grow equally well in monoculture and in mixture) are indicated by diagonal dashed lines in replacement diagrams (Fig 1). There are three possibilities, each indicating a different situation when the species are grown in mixture. (1) If the actual $RY$ curve of one species is concave and that of the second is convex, then the species compete against each other; (2) if the actual $RY$ curve of each species is convex, niche differentiation is indicated; and (3) if the actual $RY$ curves of both species are concave, then we can assume mutual antagonism. The consequences of $RYT$ values depend on whether they are equal to 1 (implying that there is competition), greater than 1 (implying niche differentiation), or lower than 1 (implying mutual antagonism) [63].

**Statistical analyses**

In the heterocarpy experiment, total mass, fruit mass and relative growth rate (RGR) were analysed with generalized linear models including Section, Invasive(Pair), Fertilization, Density, Fruit type and all second-order interactions with the exception of the interaction Fertilization $\times$ Density. All factors were considered fixed. The effects of Block and all interactions with Block were tested, and as all were non-significant ($P > 0.05$), they were dropped from the model. Total mass and fruit mass were natural log trans-formed to improve the distribution of residuals and increase the homogeneity of variance. A Gaussian distribution and identity link function were used in all analyses. Generalized linear models were carried out using R software [66]. Tukey’s post-hoc test was performed using the package multcomp (ver. 1.4–1).

In the replacement experiment, actual RY$s$ were compared to their expected values [0.25 (or 0.75) for species $i$ (or $j$) at 2i:6j proportion, 0.50 for species $i$ and $j$ at 4i:4j, and 0.75 (or 0.25) for species $i$ (or $j$) at 6i:2j] and actual RYT$s$ to their expected value (1.0) at each proportion by
t tests. Mean aggressivity values between invasive and non-invasive congeners were compared by Welch’s two sample t-tests for each phylogenetic group.

**Results**

**Heterocarpy experiment**

The generalized linear model showed no differences in total mass, fruit mass and RGR between invasive and non-invasive species (Table 2). This resulted from contradictory trait responses between invasive and non-invasive species of individual sections (Fig 2). Within the section Atriplex the invasive species *Atriplex sagittata* performed better than the non-invasive species *A. hortensis* in total mass and RGR. Within the section Sclerocalymma, however, the non-invasive *A. rosea* reached higher values of total mass and RGR than the invasive species *A. tatarica* (Fig 2).

Differences in species performance were manifested through plants growing from the ecologically most contrasting fruit types specifically for each section. In the section Atriplex, species trait differences were positively related to type A fruit (in the case of RGR) or type C fruit (in the case of total mass and RGR) (Fig 2), in no case were they related to type B fruit. In the section Sclerocalymma, species differences were found between plants arising from either type B fruit (RGR) or type C fruit (total mass and RGR) (Fig 2).

**Replacement experiment**

Actual RYs of *A. sagittata* were significantly lower than expected at two of three proportions when grown with *A. hortensis* (P ≤ 0.034) (Fig 1). While the RY of *A. rosea* was lower than

Fig 1. Results of the replacement experiment. Replacement series diagrams of two pairs of *Atriplex* congeners illustrating mean (± SE) relative yield and relative yield total as a function of species frequencies. The diagonal dashed lines are the expected relative yields when plants of species grow equally well in mixture and in monoculture. Standard error is shown if any difference from its expected value (P > 0.05) was detected. Invasive species are indicated by black triangles and non-invasive ones by white diamonds; black squares indicate total relative yield.

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expected when the species were grown at equal proportions \( (P = 0.0003) \), *A. tatarica* reached higher relative yield than expected when it grew under high population densities of *A. rosea* \( (P = 0.003) \). RYT was not significantly different from 1.0 at all proportions in these three mixture combinations for both species pairs \( (P = 0.107) \). Mean aggressivity differed significantly between the species of both pairs (Table 3). The aggressivity of the invasive *Atriplex sagittata* was significantly lower \( (P = 0.00002) \) than that of the non-invasive *A. hortensis*, but the aggressivity of the invasive *A. tatarica* was higher \( (P = 0.0009) \) than the non-invasive *A. rosea*.

**Discussion**

We analysed several life-history and functional traits of two congeneric pairs of invasive and non-invasive heterocarpic *Atriplex* species grown under different levels of nutrient supply and population density and evaluated the extent of resource partitioning between congeners. Our data support the ideas that (i) species invasiveness involves rather complex interactions of traits and is attributable to environmental and biotic factors that are resistant to generalization [11,17,18] and that (ii) heterocarpy is an important plant strategy that determines the performance of species in highly disturbed anthropogenic landscapes; in some cases, it may even contribute to species’ invasion success [43,45–47].

**Traits related to invasiveness in *Atriplex* species**

Analyses of traits indicated higher performance of invasive species relative to its non-invasive congener within the section Atriplex and showed that the invasive *Atriplex sagittata* had a higher relative growth rate on average under both fertilization levels and population densities compared to the non-invasive *A. hortensis*. Relative growth rate was positively associated with plant performance and higher photosynthetic capacity of plants [67]. The success of plant invaders has often been attributed to their capacity for fast growth [4,14,15]. Particularly in some environments, such as in disturbed and resource-rich habitats, invading fast-growing plants exploit available resources more efficiently than slow-growing natives [10,14,15].
**Fig 2. Results of the heterocarpy experiment.** Total mass, fruit mass and relative growth rate (RGR) of invasive (Inv.) and non-invasive (N-inv.) *Atriplex* species pairs representing two different sections, i.e. sect. *Atriplex* (*A. sagittata* and *A. hortensis*) and sect. *Sclerocalymma* (*A. tatarica* and *A. rosea*), compared under different fertilization levels, population densities and for plants growing from different types of fruits (i.e. A, B and C, calculated across different fertilization levels and population densities). Bars represent means ± SE; those bearing the same letter did not differ significantly (Tukey post-hoc test, \( P \leq 0.05 \)).

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We found that under higher fertilization levels the invasive \textit{Atriplex sagittata} had a greater total mass than the non-invasive \textit{A. hortensis}. \textit{Atriplex sagittata} typically colonizes various human-made habitats characterized by a high level of disturbance, low moisture and high concentrations of nitrogen [68]. Thus, the high relative growth rate and ability to maximize biomass in nutrient-rich environments predispose it to be a successful invader. This is in accordance with predictions of the fluctuating resource hypothesis, which postulated that the species' invasion success is facilitated by its ability to acquire resources under high resource availability resulting from a disturbance [19]. Compared to \textit{A. sagittata}, its non-invasive congener \textit{A. hortensis} turned out to be the better competitor when the species were grown together in the replacement series. Although this predisposes the species to overall success, there are likely some constrains which impede its escape from cultivation. One of them may be a generally low level of dormancy accompanied by high seed germinability under low temperatures [43]. In the climatic conditions of Central Europe, the majority of seeds seem to germinate in autumn and seedlings probably do not survive winter, or the majority of seeds germinate in spring and only a limited number of seeds get stored in the seed bank [43]. So, even though \textit{A. hortensis} is a heterocarpic species that should follow a so-called 'bet-hedging' strategy, its seeds are in fact ecologically equivalent and do not store part of the progeny until the next generations. Population regeneration following population failure is not effectively buffered by seeds accumulated in a seed bank, as in the case of \textit{A. sagittata}.

Surprisingly, within the section Sclerocalymma, the non-invasive \textit{Atriplex rosea} reached higher values of some traits than the invasive \textit{A. tatarica}. It had a higher relative growth rate on average across both treatments and higher total mass under low fertilization levels compared to the invasive \textit{A. tatarica}. Although \textit{A. rosea} seemed to have the potential to be more invasive on the basis of an analysis of life-history traits, it has currently disappeared from Central Europe. However, it was a relatively common species at the beginning of the 20th century, when it typically occurred on rural farms and in villages with numerous fowl runs, which are rare today [44]. Today, it is invasive in certain parts of southwestern North America, where it is a widely established weedy species of disturbed sites, often occurring in riparian habitats, barnyards, animal bed grounds and along roadsides [69]. Its congener \textit{A. tatarica}, which in the past occupied similar habitats as \textit{A. rosea} [44], is currently spreading north along roads also in areas that are quite cold for species with C\textsubscript{4} photosynthesis such as central and northern Poland and Germany [70,71]. Both species of the section Sclerocalymma are salt-tolerant weak competitors inhabiting open habitats where competitive pressure of other plant species is reduced to a minimum. This adaptation might be crucial mainly in cases of spreading along roads treated with salt in winter. After we planted both species together in the replacement series, we observed that \textit{A. tatarica} reduced the final biomass of \textit{A. rosea} and proved to be a stronger competitor. Assuming there are no differences in habitat preferences or germination
requirements [43] between the two species, the competitive superiority of *A. tatarica* could favour it over *A. rosea* in alternate habitats and perhaps explain its current progressive tendency to spread in parts of Central Europe.

To sum up, even though we compared two pairs of phylogenetically closely related invasive and non-invasive species that largely share the same reproductive biology, growth form and habitat preferences, the results concerning traits shared by invasive species are inconclusive. The fact that we did not detect any general relationship between invasive status and individual traits is particularly surprising, given how similar and in a certain sense comparable the study species are with respect to their phylogenetic proximity, life history type and growth form. We therefore conclude that even though congeners offer the best available methodical framework for comparing traits among similar species, this approach might not be suitable for identifying invasive traits because of the complexity underlying invasiveness.

**Heterocarpy**

Annual representatives of the genus *Atriplex* are usually heterocarpic and follow a bet-hedging strategy, as previously documented for many *Atriplex* species [35,43–47,72–77]. Although some aspects of particularly earlier phases of the life cycle (i.e. germinability and dispersibility) were frequently addressed in previous studies, traits closely related to the performance of individuals originating from different fruit types were hardly explored at all (but see [47,78]). More extensive evidence comes from studies on species of the family Asteraceae, supporting differences in, for example, survival, growth, competitive ability, life history and demographic characteristics (see [21–23] and references therein).

Our analysis revealed similar patterns of traits for members of *Atriplex* species. Plants growing from particular fruit types differed in their allocations to plant biomass and relative growth rate, but the differences were both species- and trait-specific (Fig 2). More interestingly, we found consistent trait differences between plants growing from different fruit types, which might explain the invasion success of some heterocarpic *Atriplex* species. We showed that differences in trait characteristics positively related to species invasion success are always associated with type C fruit or sometimes with type A fruit, but never with type B fruit. This trend was conspicuous for species of the section *Atriplex* having three types of fruit that are ecologically differentiated. It seems that fruit types with contrasting ecological behaviours play important roles in the process of invasion or, more generally, in the spreading of any heterocarpic species in a variable environment. This may be realized through maximizing population growth (via plants growing from the highly abundant non-dormant type C fruit) and by enhancing the likelihood of establishing a new population after a major disturbance (via plants arising from the deeply dormant type A fruit). Several studies dealing with heterocarpy within the genus *Atriplex* have demonstrated its important role for overall species performance in a wide range of conditions and under intensive disturbances of human-made habitats [40,41,43,45–47]. The specific roles of different fruit types determining species success have been clarified especially in the case of *A. sagittata*, which has three types of fruit that differ in their germination and dispersal characteristics [43,45]. Type A (ebracteate) fruit is deeply dormant and has the lowest dispersibility. Of the two more dispersible fruit types with bracts, type B fruit exhibits a certain degree of dormancy whereas type C fruit is non-dormant [46]. While at least a portion of dormant types A and B fruits remain in the seed bank, ensuring long-term species survival in a highly disturbed environment, the most abundant non-dormant C fruits germinate immediately when conditions become favourable. Mandák and Pyšek [41], with regard to dormancy patterns, stated that the success of *A. sagittata* in the present Central European landscape might, at least partly, be attributed to its heterocarpy and associated plastic
response to changing environmental conditions. However, comparing different species exhibiting different degrees of success in today’s countryside could disentangle the exact role of heterocarpy in this annual plant species. We have shown that heterocarpy is important, but in different phases of the plant life cycle in different species, depending on the behaviour of heterocarpic morphs. Baskin et al. [22] pointed out this knowledge gap and showed this in their review of heteromorphic species of cold deserts of northwest China. They stated that heterodiaspory is without doubt a significant adaptation in cold desert annuals. We suggest that heterocarpy in the sense of preadaptation to cold desert environments constitutes a set of complex adaptations which may predispose species to successful establishment and invasions in a wide range of habitats and under intensive disturbances typical of man-made landscapes. However, to generalize these results, studies involving more model groups with different levels of heterocarpy and invasive status should be performed.

Conclusions
The main result of this study is that in a comparison of life history traits of two species pairs, the relative importance of heterocarpy, as opposed to other biological aspects in the current invasion success of closely related Atriplex species, clearly differs. Whilst differences in biomass production and growth characteristics could explain the current invasibility of A. sagittata, invasive species had surprisingly lower competitive ability. Interestingly, the differences between species were manifested in plants growing from the ecologically most differentiated fruit types. On the other hand, the invasive success of A. tatarica, which reached lower overall growth rates than its congener A. rosea, is attributable to its higher competitive ability or other, as yet unknown, biological aspects associated with its ability to occupy alternate habitats. Hence, the invasive species under study did not differ in functional traits from non-invasive ones across the sections, supporting the notion that species invasiveness involves more complex interactions of traits that may be important only in certain contexts. Specific species-habitat interactions are therefore very important for determining species invasiveness. This view is also supported by the outcomes of current invasion biology [11,17,18], pointing out that invasibility is rather resistant to generalization. Thus, the study of congeners is unlikely to reveal traits responsible for invasiveness because of the complexity underlying the whole invasion process.

Supporting information
S1 Dataset. Data from heterocarpy experiment.
(XLSX)

S2 Dataset. Data from replacement experiment.
(XLSX)

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