

Effect of residence time on trait evolution in invasive plants: review and meta-analysis

Michal Gruntman¹, Udi Segev^{2,3}

1 School of Plant Sciences and Food Security and Porter School of the Environment and Earth Sciences, Tel Aviv University, P.O. Box 39040, Tel Aviv 6997801, Israel **2** Department of Natural Sciences, The Open University of Israel, 1 University Road, P.O. Box 808, Raanana 43107, Israel **3** The Entomological Lab for Applied Ecology, The Steinhardt Museum of Natural History, Tel Aviv University, P.O. Box 39040, Tel Aviv 6997801, Israel

Corresponding author: Michal Gruntman (michal.gruntman@gmail.com)

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Abstract

The success of invasive species is often attributed to rapid post-introduction evolution, due to novel selection pressures at the introduced range. However, evolutionary shifts in invasion-promoting traits can also take place within the introduced range over time. Here, we first present a review of the proposed hypotheses regarding the selection pressures and trait divergence along gradients of invasion history and the studies that examined them. In addition, we present the results of a meta-analysis aimed to provide a more general overview of current knowledge on trait evolution with time since introduction. Invasion-promoting traits, including growth, competitive ability and dispersal ability, were proposed to decline in more established populations with a long invasion history due to the attenuation of selection pressures, such as enemy release or interspecific competition, while herbivore defence was suggested to increase. Our meta-analysis results reveal a general indication for the evolution of invasive plants with residence time for most of the studied traits. However, this divergence did not have a consistent direction in most traits, except for growth, which, in contrast with our prediction, increased with residence time. The lack of empirical support for the predicted change in most of the studied traits over time suggests trait evolution might be affected by other context-dependent factors such as climatic gradients along invasion routes. Similarly, the increased allocation to size in older and more established populations may be driven by increased conspecific competition pressure experienced in these populations. The general temporal effect found in our meta-analysis stresses the need to consider population age when comparing attributes of invasive plants between native and invasive ranges. Moreover, the increased size of invasive plants in older populations, suggests that the dominance of these plants might not attenuate with time since introduction, thus highlighting the need to further explore the long-term dynamics between invasive plants and their recipient native communities.

Keywords

Chronosequence, enemy release hypothesis, evolution of competitive ability hypothesis, invasive plants, novel weapons hypothesis

Introduction

A main interest in the study of plant invasion is the characterisation of traits associated with invasive success, such as high growth rate, competitive ability and phenotypic plasticity and the processes governing the prevalence of these traits in introduced compared to native ranges (Baker 1965; Thébaud and Simberloff 2001; Vila and Weiner 2004; Blumenthal and Hufbauer 2007; Pyšek and Richardson 2008; Van Kleunen et al. 2010; Hodgins et al. 2018). While traits that determine invasiveness could be pre-selected for invasion (Schlaepfer et al. 2010), the success of invasive species has often been attributed to rapid post-introduction evolution, due to novel selection pressures at the introduced range, such as release from native enemies and co-evolved competitors (Blossey and Notzold 1995; Sakai et al. 2001; Keane and Crawley 2002; Callaway and Ridenour 2004; Bossdorf et al. 2005; Prentis et al. 2008). Such trait evolution in invasive plants has been examined in ample studies that provided support for evolutionary shifts between native and introduced ranges in traits such as defence, growth, fecundity, competitive ability, allelopathy and phenotypic plasticity (see meta-analyses: Thébaud and Simberloff (2001); Davidson et al. (2011); Felker-Quinn et al. (2013); Rotter and Holeski (2018); Zhang et al. (2018)).

In addition to trait divergence between the native and introduced ranges, evolutionary shifts in invasion-promoting traits can take place within the introduced range over time, due to varying selection pressures that might come into play at different invasion stages (Siemann et al. 2006; Strayer et al. 2006; Lankau 2011; Dostál et al. 2013; Gruntman et al. 2017). For example, while populations at the invasion front can experience release from enemies or co-evolved competitors, this selection pressure is likely to attenuate over time in fully-established populations, where herbivores and pathogens could become increasingly accustomed to the invasive plant (Hawkes 2007; Brändle et al. 2008; Diez et al. 2010; Mitchell et al. 2010; Dostál et al. 2013; Flory and Clay 2013) and intraspecific competition could intensify (Inderjit et al. 2011). Such changes in selection pressures might, in turn, lead to divergence in invasion-promoting traits along gradients of invasion history, with attributes that facilitate greater invasion potential in populations at the invasion front, compared to core populations.

Compared to the evolution of invasive plants between their native and introduced ranges, fewer studies have looked at potential evolutionary shifts within the introduced range. However, studying the idea that invasive plants might undergo rapid selection with time since their introduction might provide a unique model system to explore fundamental questions related to adaptive divergence in plant traits. Moreover, if the adaptive advantage of invasion-promoting traits might decline in more established populations with a long invasion history, this might lead to changes in the effect of

such invasive plants on local communities (Strayer et al. 2006; Dostál et al. 2013; Pyšek et al. 2015; Crystal-Ornelas and Lockwood 2020). Hence, knowledge on the potential evolution of invasive populations at different invasion stages might also be valuable for predicting the long-term effects of invasive plants and evaluating alternative management practices (Strayer et al. 2006; Wilson et al. 2007; Bucharova and Van Kleunen 2009).

Studying the evolution of invasion-promoting traits with time since introduction presents a challenge, as knowledge on population ages and residence times might not be readily available. However, despite these difficulties, an increasing number of studies have recently focused on exploring changes in invasion-promoting traits of invasive plants over time (Suppl. material 1: fig. S1). Here, we first present a review of the proposed hypotheses regarding the selection pressures and evolution of trait divergence along gradients of invasion history and the studies that examined them. In addition, we present the results of a meta-analysis aimed at providing a more general overview of current knowledge on trait evolution with time since introduction. In both the review and meta-analysis, the chosen species were defined as “invasive” according to the definition of the CBD, i.e. alien species that threaten ecosystems, habitats or species (CBD 2000).

Review of trait evolution with invasion history

Approaches for studying trait divergence in invasive species over time

Two main approaches have been employed to study changes in invasion-promoting traits over invasion-history gradients, with advantages and drawbacks to both. In the first approach, plant traits are compared amongst different invasive species with varying residence time within a region (e.g. Hawkes (2007); Iacarella et al. (2015); Sheppard and Schurr (2019); Sheppard and Brendel (2021)). Such an interspecific approach can provide a generalised overview across multiple species and requires only general knowledge on residence time of species within a region, such as the earliest report of introduction time (e.g. at the country level). However, results of multi-species experiments might be confounded due to historic biases in the types of introductions (Sheppard and Brendel 2021) or due to discrepancies between the time of introduction to certain regions and the age of the sampled populations (but see Iacarella et al. (2015)). In the second approach, plant traits are compared within a species across different populations along gradients of invasion history (e.g. Lankau et al. (2009); Gruntman et al. (2017); Tabassum and Leishman (2018)). This intraspecific approach requires knowledge on population age (a chronosequence approach) or the identity of source populations and invasion trajectories (i.e. distance to source populations), as well as information on the possibility of multiple introductions. Regardless of the approach used, the study of divergence in invasion-promoting traits is best examined in controlled common garden experiments, which expose plants with varying invasion

histories to the same environmental conditions. Such studies can reveal inherent variations in trait levels and exclude variations due to plastic responses to field conditions at different sites.

Two additional approaches should be noted due to the alternative advantages they offer to the study of trait evolution along invasion-history gradients. The first approach is the use of herbaria collections, which can provide historical samples of invasive plants (reviewed in: Meineke et al. (2018); Lang et al. (2019)). Such collections can be compared at the intraspecific level to identify divergence over time since introduction in physiological and morphological traits, such as herbivore defence compounds or plant size (Zangerl and Berenbaum 2005; Buswell et al. 2011). Herbaria records can, thus, be an important tool in the study of invasion history. The second approach is the use of selection gradients (Lande and Arnold 1983) on invasion-promoting traits, which are measured in the field in introduced populations with different invasion histories. Such field measurements of selection can provide important knowledge on the adaptive relevance of a focal trait in different populations along invasion gradients, but, to date, it has mainly been applied to study variations between native and introduced populations (e.g. Franks et al. (2008); O'Donnell and Pigliucci (2010); Colautti and Lau (2016)). However, as for other studies using field-collected measurements or samples, both approaches cannot exclude plastic responses to field conditions as an explanation for trait variation rather than evolutionary change (excluding herbaria studies that examine the genetic makeup of plants: Vandepitte et al. (2014)).

The following sections provide a review of the hypotheses suggested to explain the effect of time on the evolution of different invasion-promoting traits, including defence, growth, competitive ability and dispersal ability, focusing on studies that examined them under common garden conditions.

Divergence in traits associated with defence

One of the most well-studied hypotheses to explain the success of invasive plants is the evolution of increased competitive ability hypothesis (EICA) (Blossey and Notzold 1995). This hypothesis proposes that plants in their introduced range experience reduced damage by natural enemies, such as pathogens and specialist herbivores, which selects for reduced allocation to defence traits and a consequent increase in resources available for growth and competitive ability (Blossey and Notzold 1995; Bossdorf et al. 2005). Alternatively, the shifting defence hypothesis (SDH) proposes that the loss of specialist enemies at the introduced range can result in an evolutionary shift from investment in defence against specialists (digestibility reducers such as trichomes and tannins) to defence against generalists (toxins such as glucosinolates and alkaloids) (Müller-Schärer et al. 2004; Joshi and Vrieling 2005).

Both the EICA and the SDH assume that invasive plants experience release from their specialist enemies at the introduced range. This attenuating selection pressure is not likely to change with time since introduction, except due to the unintentional introduction of specialist herbivores or pathogens (e.g. Zangerl and Berenbaum (2005);

Wan et al. (2019)) or their use as biocontrol agents (Stastny and Sargent 2017). Nevertheless, several studies have shown that enemy pressure on invasive plants increases over time. In particular, more established populations have been shown to experience greater colonisation rates and attacks from local herbivores (Hawkes 2007; Brändle et al. 2008; Dostál et al. 2013; Harvey et al. 2013; Schultheis et al. 2015; Gruntman et al. 2017; but see Carpenter and Cappuccino (2005)), increased pathogen accumulation (Siemann et al. 2006; Hawkes 2007; Mitchell et al. 2010; Flory and Clay 2013) and increased negative soil feedback (Diez et al. 2010). These results imply that compared to range-edge populations, older populations might incur greater attacks even from generalist enemies. Such increased enemy load could be attributed to increases in the density and abundance of invasive plants in older populations, which could increase their attraction as hosts (Agrawal et al. 2006).

Increased enemy pressure with time since introduction might re-select for increased allocation to defence traits in plants and particularly against generalist herbivores (Fig. 1). However, we are aware of only three studies to date that examined divergence in defence-related traits along invasion history gradients under common garden conditions. Gruntman et al. (2017) found that *Impatiens glandulifera* plants from younger populations within the invasive range have reduced herbivore resistance against a generalist herbivore, coupled with reduced production of secondary defence compounds, to an extent similar to those of native populations. In contrast, Siemann et al. (2006) found no effect of population age on *Sapinum sebiferum* survival in common gardens exposed to local herbivores, even though herbivory levels increased in older populations. Similarly, Harms and Walter (2021) found no effect of population age on herbivore defence against a generalist herbivore in the invasive plant *Butomus umbellatus*. Additional studies are, therefore, required to provide a general understanding of the effect of invasion history on the evolution of enemy defence in invasive plants. Moreover, such future studies should compare their relative allocation to defence against specialist vs. generalist enemies across populations with different invasion histories.

Divergence in growth traits

Invasive plants are commonly associated with increases in growth rate and size at their introduced compared to native range (Pyšek and Richardson 2008; Van Kleunen et al. 2010). While such increases in growth-related traits can be a result of plastic responses to the environment, they might also be attributed to evolutionary change. The latter idea was proposed in the EICA hypothesis, which predicts that, due to an allocation trade-off, the decrease in defence experienced by plants at the introduced range is likely to result in an evolutionary increased allocation to traits related to growth (Blossey and Notzold 1995; Bossdorf et al. 2005; Joshi and Vrieling 2005). The same defence-growth trade-off might govern the evolution of growth traits within the introduced range of invasive plants. Specifically, if as suggested above, older and more established populations incur more enemy pressure that selects for increased investment in defence, these populations are also predicted to evolve decreased allocation to growth (Fig. 1).

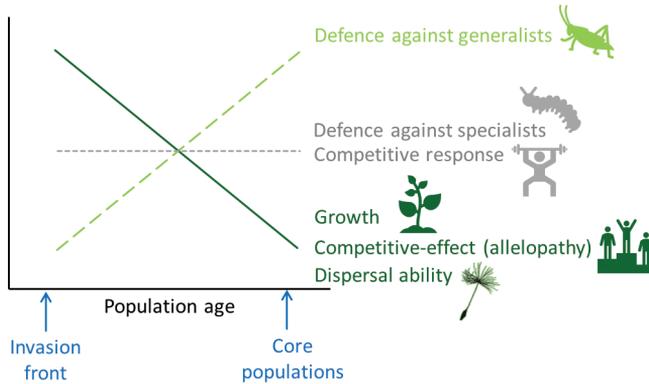


Figure 1. Schematic representation of the predicted effect of population age on divergence in different invasion-promoting traits, including positive effects (light green), negative effects (dark green) and no effect (grey).

We found seven common garden studies that explicitly investigated the effect of invasion history on the evolution of plant growth and their results provide contrasting patterns. Kilkenny and Galloway (2013) and Evans et al. (2013) provide support for the hypothesised negative effect of invasion history on plant size in studies on the invasive plant *Lonicera japonica*, where plants from core populations within the introduced range were smaller than their conspecifics from edge populations. In contrast, Wan et al. (2018) found that *Plantago lanceolata* plants from populations with a long invasion history were larger and more fecund compared to populations at the invasion front and similar results were shown by Fenesi and Botta-Dukát (2012) in *Ambrosia artemisiifolia* and VanWallendael et al. (2018) in *Reynoutria japonica*. Finally, Monty and Mahy (2009) found no effect of population age on biomass production of *Senecio inaequidens* and Tabassum and Leishman (2018) similarly found no effect of distance to source population on the height of *Gladiolus gueinzii*.

A lack of consistent results regarding the effect of invasion history on plant size might reflect the variety of selection pressures that likely act on such a fundamental life-history trait. For example, local climate across elevational and latitudinal gradients, as well as levels of primary productivity, might also change along invasion routes and exert strong selection on plant size and growth rate (Colautti et al. 2009; Monty and Mahy 2009). Thus, although the defence-growth trade-off might be key to the invasive success of many plant species, other factors can contribute to divergence in growth traits within the introduced range.

Divergence in traits associated with competitive ability

Two hypotheses were suggested to account for the evolution of competitive ability in invasive plants and can be similarly applied for divergence in competitive ability within the introduced range. First, as suggested above and following the premise of the EICA

hypothesis, older populations are predicted to undergo selection for increased defence associated with decreased allocation to growth and plant size. This decrease in size is, therefore, likely to be manifested in reduced competitive ability via resource competition in older and more established populations. In contrast, populations at the invasion front are predicted to undergo selection for decreased defence and increased size and competitive ability.

The second hypothesis suggested to explain the evolution of increased competitive ability in invasive plants is the novel weapons hypothesis (NWH: Callaway and Aschehoug (2000); Callaway and Ridenour (2004)). The NWH suggests that the production of toxic allelochemicals should be selected for in introduced populations due to its enhanced negative effects on naïve native competitors compared to co-evolved ones at the native range (Callaway and Ridenour 2004; Prati and Bossdorf 2004; Abhilasha et al. 2008). Hence, this hypothesis proposes increased selection for competitive ability via interference competition in introduced populations. As for plant size and its derived competitive ability, the adaptive advantage of allelopathy might also decline with time since introduction, due to three selection pressures. First, the above-suggested need for increased production of defence compounds in older populations, might favour decreased production of allelochemicals due to a trade-off between these secondary compounds (Inderjit et al. 2011; Gruntman et al. 2017). Secondly, in older and more established populations, plants might experience a shift from competition with heterospecific to conspecific neighbours, which are usually unaffected by conspecific allelochemicals (Inderjit et al. 2011). Thirdly, with time since introduction, co-occurring native species or their mutualist soil biota might also evolve resistance to the novel allelochemicals of the invasive plants (Callaway et al. 2005; Lankau 2011; Dostál et al. 2013).

Competitive ability can be attributed to two components that were suggested to be associated with different traits (Goldberg 1990, 1996). Competitive effect, which is the ability to suppress neighbours, can be attributed to rapid resource acquisition and growth or to allelopathy; while competitive response, which is the ability to withstand competition, can be attributed to tolerance of low resource levels or to neighbour avoidance (Goldberg and Landa 1991; Cahill et al. 2005). Thus, the two aforementioned hypotheses regarding the evolution of decreased competitive ability with time since introduction via allocation to plant size or allelopathy, are mostly related to competitive effect (Fig. 1). In contrast, competitive response might be either not affected by these processes or even increase, if lower growth rate and smaller size correlate with stress tolerance (Fig. 1).

Changes in competitive ability at the introduced range over time were examined in several studies. Some of these studies used an interspecific approach and examined the competitive effect of multiple invasive species with different residence times, using either common garden experiments (Sheppard and Schurr 2019; Sheppard and Brendel 2021) or a meta-analysis approach (Iacarella et al. 2015) and their results reveal different patterns. For example, Sheppard and Brendel (2021) used a common garden experiment to study the competitive effect of 47 non-native Asteraceae species on native plants and found that species with longer residence time had stronger competitive effects. However,

this study referred to plants of varying non-native status rather than strictly invasive species and the variation in their competitive effect was better explained by this status (casual vs. established neophytes, archaeophytes or native species). In contrast, Iacarella et al. (2015) performed a meta-analysis of studies that examined the competitive effect of 36 invasive species with a known residence time at the collection sites and found that competitive effect of the plants decreases with time since introduction. The results of this study provide compelling evidence for temporal shifts in the evolution of competitive ability, because they are based on introduction time of the studied population rather than the entire invaded region. However, such an interspecific approach might be confounded due to variations in competitive ability amongst species, which can be avoided by comparing competitive ability of conspecifics with different residence time.

A few common garden studies used an intraspecific approach and explored divergence in competitive ability amongst populations of the same species across invasion gradients. While some of these studies have attributed competitive ability to growth traits, such as plant height and biomass (see “Divergence in growth traits” above), we found only six studies that have explicitly examined divergence in competitive ability and all compared competitive effects on the performance of neighbours or the production of allelochemicals. Lankau et al. (2009) and Lankau (2012) provide support to the predicted decrease in competitive effect with invasion age, showing that the production of allelochemicals in invasive *Alliaria petiolata* declines in older populations. Similarly, Oduor et al. (2022) found that invasive *Solidago canadensis* plants from older populations had a lower competitive effect on native species and a greater competitive response to them, although these interactions depended on plant-soil feedbacks, suggesting that soil biota has an important role in these interactions. Evans et al. (2013) also found a reduced competitive effect in older *Lonicera japonica* populations under competition with conspecifics. In contrast, Huang and Peng (2016) found that the competitive effect of the invasive vine *Mikania micrantha* in intraspecific competition is higher in more established core populations, while Gruntman et al. (2017) found no effect of population age on allelopathic ability of invasive *Impatiens glandulifera*.

The lack of consistent results for the effect of invasion history on the competitive ability of the studied plants might be attributed to variations in competitive environments experienced by these plants. For example, as suggested above, invasive plants often experience a shift from inter- to intraspecific competition with time since introduction, which could select for different competitive strategies. Indeed, in this review, the three studies whose results support the predicted decrease in competitive effect used heterospecific neighbours, while a study that employed conspecific competitors found the opposite trend (Huang and Peng 2016). Further studies are, therefore, needed to differentiate between the effect of invasion history on inter- vs. intraspecific competitive ability.

Divergence in dispersal ability

As for other invasion-promoting traits, evolution of traits related to dispersal ability might also take place between different invasion stages within the introduced range. The most common hypothesis in this regard proposes that, during range expansion, higher dispersal

ability is likely to be selected for in individuals arriving at the invasion front compared to core populations (Hargreaves and Eckert 2014; Hodgins et al. 2018) (Fig. 1).

The notion that dispersal ability should be selected for at range edges of invasive species has been suggested in several theoretical models (Travis and Dytham 2002; Phillips et al. 2008; Travis et al. 2009) and supported by several studies on invasive animal species (e.g. Hughes et al. (2003); Phillips et al. (2006); Lombaert et al. (2014); Ochocki and Miller (2017)). However, evolutionary shifts in dispersal ability at range edges of invasive plants have been relatively less studied, of which we are aware of only two studies that were conducted with seeds collected from plants grown under common garden conditions. These studies, by Monty and Mahy (2010) and Huang et al. (2015), provide support for increased dispersal ability (i.e. increased investment in seed pappus) at the invasion front of the invasive plants *Senecio inaequidens* and *Mikania micrantha*, respectively. A few additional studies examined dispersal ability in seeds that were collected directly from field populations and not from plants growing under common garden conditions, showing similar results (Tabassum and Leishman 2018; Robinson et al. 2023; but see Bartle et al. (2013)).

In summary, accumulating evidence provides support for different ways in which invasion-promoting traits such as defence, growth, competitive ability and dispersal might evolve in the introduced range over time. However, our review of the studies did not reveal consistent directions in divergence for most of the studied traits, which could be attributed to other selection pressures that might vary along invasion gradients. Moreover, existing studies that have explicitly explored trait divergence along gradients of invasion history are still very few, ranging from two to seven studies per trait, thus precluding our ability to reach generalised conclusions and highlighting the need for further studies on the subject. The aim of the following meta-analysis is to provide a more general overview on the subject.

Meta-analysis of trait divergence with invasion history

Studies that examine divergence in plant characteristics with residence time often vary in the specific traits and the methodology used to measure them, as well as the way residence time is evaluated and compared across populations. For example, different studies used either time of introduction or distance from core population(s) to estimate chronosequence effects. Therefore, to provide a more general overview of current knowledge on trait divergence with time, we employed a meta-analysis approach that synthesises published literature on the subject. However, as apparent from the literature review above, only very few studies compared trait variations of invasive populations across invasion gradients and even fewer compared these traits under common garden conditions, rendering the data insufficient from which to draw conclusions. To tackle this issue, we employed an additional approach in our meta-analysis, whereby we analysed data from common garden experiments that measured invasion-promoting traits across several populations and used information on the age of these populations from additional sources.

Using the two approaches, we asked whether invasion-promoting traits, including herbivore defence (in general or against generalist or specialist species if known), plant growth, competitive ability (effect and response) and dispersal ability, change with residence time across populations of the same invasive plant species. In addition, we asked whether such an overall change has a similar direction within or across traits, corresponding to the predictions outlined above, including an increase in defence, particularly against generalist herbivores; and a decrease in growth, competitive ability, particularly competitive effect, and dispersal ability (Fig. 1).

Methods

Literature search

To test for directional changes in the different traits along the invasion-history gradient, we used two literature review procedures. In the first procedure, we searched for studies explicitly investigating divergence in plant characteristics along invasion gradients at the introduced range, which included information on population ages. The literature was searched using two databases, Web of Science Core Collection (WOS) and Google Scholar. We first screened the literature in WOS (last accessed on 17 January 2023), using the search terms (chronosequence OR time-since-introduction OR invasion-history OR residence-time OR range-expansion OR colonization-history OR introduction-history) AND (plant*) AND (invasi*). We then complemented our search and screened the literature in Google Scholar (last accessed on 6 July 2022), using similar search terms.

Papers selected for the analysis had to meet the following criteria: (1) the study aimed to test the relationship between residence time of an invasive plant and at least one of the following traits: defence against herbivores (measured as, for example, the inverse of leaf damage or herbivore mass following feeding or the production of defence metabolites), plant growth (e.g. plant biomass or height), competitive effect (e.g. effects on the performance of native species or allelopathy), competitive response (e.g. performance of the invasive species under competition with native species) and dispersal ability (e.g. the ratio between the size of dispersal structures such as wing or pappus and seed mass); (2) a gradient of invasion history was explicitly reported in the paper, either as differences in time (generally in years, although papers that reported residence times at large geographical scales, such as country were not included) or as a distance from source to expanding populations; (3) the study reported the results of controlled experiments under common garden conditions, thus ensuring that variations amongst populations in the studied traits are the result of genetic differentiations rather than plastic responses to environmental conditions at the site. A total of 24 cases from 19 papers were included after meeting these criteria.

We carefully checked whether species were defined as invasive (rather than, for instance, alien or naturalised), based on the terminology given in the specific studies as well as in the CABI compendium digital library, invasive species section

(<https://www.cabidigitallibrary.org/product/qi>). Moreover, in several cases, in which naturalised vs. invasive ranges of introduced species were compared, only the invasive range was used in our analysis.

In the second literature review procedure, we searched for studies investigating variation in characteristics of invasive plants across populations under common garden conditions, but that did not explicitly include data on invasion history. Instead, these data were extracted from additional sources. The literature was searched using the Web of Science Core Collection (WOS) (last accessed on 18 January 2023), using the search terms (common garden OR greenhouse) AND (population OR accession) AND (plant*) AND (invasi*). Data on the location of the collection sites used in the different studies were extracted when possible. Invasion history of the populations was obtained when possible from additional papers that studied the same populations. For other cases, this information was extracted from additional sources such as the Global Biodiversity Information Facility database (<https://www.gbif.org/>) and CABI compendium digital library- invasive species section. Such information was extracted only for the same locations or for nearby locations at the scale of kilometres. In cases where information on the age of certain populations was missing, such populations were excluded from the analyses. Moreover, when information was given in the literature on the location of the first introduction of the invasive plant (given mostly at the local scale, for example, city), this location was used to estimate the distance from the source population with Google Earth Pro. In such cases, distance to source population was used instead of population age in the analysis. Papers selected for the analysis had to meet similar criteria as in the first literature review procedure, with the exception that information on population ages was not provided, but could be extracted from external sources, following which a gradient of invasion history was used to compare across sites.

Using the two literature review procedures, a total of 79 cases from 62 papers were included after meeting our inclusion criteria in the final dataset of the meta-analysis (see Suppl. material 1: fig. S2 for more details on paper screening and selection process).

Data analysis

Data on the relationship between invasion history (population age or distance from source population) and the studied traits were extracted for each of the selected study cases. When source data were not available, the data were extracted from figures using the software GetData Graph Digitizer ver. 2.26 (<http://getdata-graph-digitizer.com>). In studies where several treatments were applied (e.g. water or nutrients addition or different disturbance levels), only a subset of the data, representing standardised controlled conditions, was used, such as high water availability (see Suppl. material 1: table S1 for details on specific studies).

As considerable variation could be found amongst studies in the ranges of ages or distances across the studies populations, both the invasion history and measured trait data were first transformed using *z*-standardisation (standardised by subtracting the mean from each value and dividing by the standard deviation). A linear regression was then performed between the measured trait values and population age/distance.

The standardised slope of the regression (β) was taken as the estimated effect size and the variance of the estimate of the standardised slope (SE squared) was taken as the estimated sampling variance (see Suppl. material 1: table S1). When other geographic variables were provided for the populations, such as elevation or mean annual temperature, the estimated standardised slope and variance were generated using linear model or linear mixed model analyses, with these variables as covariates (see Suppl. material 1: table S1).

The effect of invasion history on overall trait divergence (regardless of its direction) was examined with the absolute value of the estimated standardised slope ($|\beta|$), while the effect on directional changes in traits was examined with the standardised slope (β) as an effect size. For both meta-analyses, a random-effects model was used in order to combine the estimated effect sizes from the different studies. Such random-effects models allow for both variation of effect sizes amongst studies and sampling variation within studies (Koricheva and Hayes 2018). In order to estimate model parameters, a Restricted Maximum Likelihood (REML) approach was used. In order to determine means and confidence intervals for the different trait categories, trait category was used as a moderator in the models. As some studies used the same invasive plant species or different traits were sometimes measured in the same study (see Suppl. material 1: table S1), study as well as species identity were also included as random factors in the models. Effect sizes were considered significant if the 95% confidence intervals did not overlap zero. Meta-analyses were performed using the METAFOR package v.4.4 (Viechtbauer 2010) in R-Studio v.2023.9.1.494 (Posit team 2023) and R (R Core Team 2023).

Effects of type of study and origin of information on effect sizes

Study cases selected for the meta-analyses included information on invasion history data extracted from different sources, i.e. reported in papers ($n = 36$ cases) or estimated from external databases ($n = 43$). In addition, invasion history was measured in two ways, i.e. residence time ($n = 65$) or distance from source populations ($n = 14$) (Suppl. material 1: table S1). A meta-regression model was, therefore, conducted to assess the effect of these moderators on the magnitude of effect sizes. Here, a random-effects meta-regression was performed, in which data origin and type of study were served as moderators, study as well as species identity were included as random factors and an REML approach was employed to estimate model parameters. To interpret the significance of the chosen moderators, Q_m statistics was used to test the extent of heterogeneity explained by the moderators. The meta-regression was performed using the METAFOR package v.4.4 (Viechtbauer 2010) in R-Studio v.2023.09.1.494 (Posit team 2023) and R (R Core Team 2023).

Publication bias analysis

The magnitude and significance of effect sizes may affect the publication and/or visibility rates of studies (e.g. based on the impact factor of journals) (Koricheva et al. 2013). To test for a possible publication bias in cases where the overall effect sizes in our meta-analyses were found to be significant, several approaches were used. First, we

tested for temporal publication bias, examining a potential correlation between effect sizes and publication year. Additionally, we checked for a potential correlation between effect sizes and the journal's impact factor at the year of publication. We also tested for the possibility that differences in age and distance ranges amongst studies could influence effect sizes. To that end, an LMM analysis was used, in which publication year, journal's impact factor and age/distance ranges per study served as the independent variables and study identity and the invasive plant species served as random factors. Finally, we estimated the fail-safe numbers using the Rosenberg method (Rosenberg 2005), which indicates the number of additional studies with effect size of 0 needed to reduce the significance level of the observed average effect size to $\alpha = 0.05$. This analysis was conducted using the Fail-Safe Number Calculator software (<https://www.rosenberglab.net/Rosenberg2005FailSafe.html>). Statistical analyses, unless indicated otherwise, were performed using JMP Pro 17.1 (SAS Inst. Inc.).

Meta-analysis results

A total of 79 observations from 62 studies were included in our meta-analysis after meeting our criteria (Suppl. material 1: table S1). Population age in these studies ranges between 0 and 230 years and distance from source to peripheral populations ranges between 0 and 1000 km (Suppl. material 1: table S1). Overall, invasive species exhibited divergence in the studied traits over time, when averaged across traits ($p < 0.001$, Fig. 2A). This overall change is also shown for traits related to defence ($p < 0.001$) and defence against generalists ($p < 0.007$), growth ($p < 0.001$), dispersal ability ($p = 0.023$), overall competitive ability ($p < 0.001$) and competitive effect ($p < 0.001$), but not for defence against specialists ($p = 0.146$) or competitive response ($p = 0.363$) (Fig. 2A).

In contrast to the overall trait divergence, the direction of change was not affected by residence time for most trait categories, including overall defence ($p = 0.135$), competitive ability ($p = 0.95$) or dispersal ability ($p = 0.105$) (Fig. 2B). However, plant growth increased with residence time (estimated slope \pm SE = 0.187 ± 0.057 ; $p = 0.001$; Fig. 2B).

Effects of type of study and origin of information on effect sizes

The meta-regression results indicate no significant effect of the two moderators on absolute effect sizes ($Q_M = 3.193$, $p = 0.203$, residual heterogeneity $Q_E = 162.94$, $p < 0.001$). Specifically, there were no significant differences in absolute effect size between the two types of study (residence time: mean \pm SE = 0.272 ± 0.041 ; distance: mean \pm SE = 0.334 ± 0.084 , $p = 0.48$; Suppl. material 1: fig. S3). Yet, a non-significant trend was found for the origin of data, according to which absolute effect size values of data reported in papers was slightly higher than data estimated using external databases (reported in papers: mean \pm SE = 0.369 ± 0.085 ; estimated from external sources: mean \pm SE = 0.247 ± 0.097 , $p = 0.075$; Suppl. material 1: fig. S3).

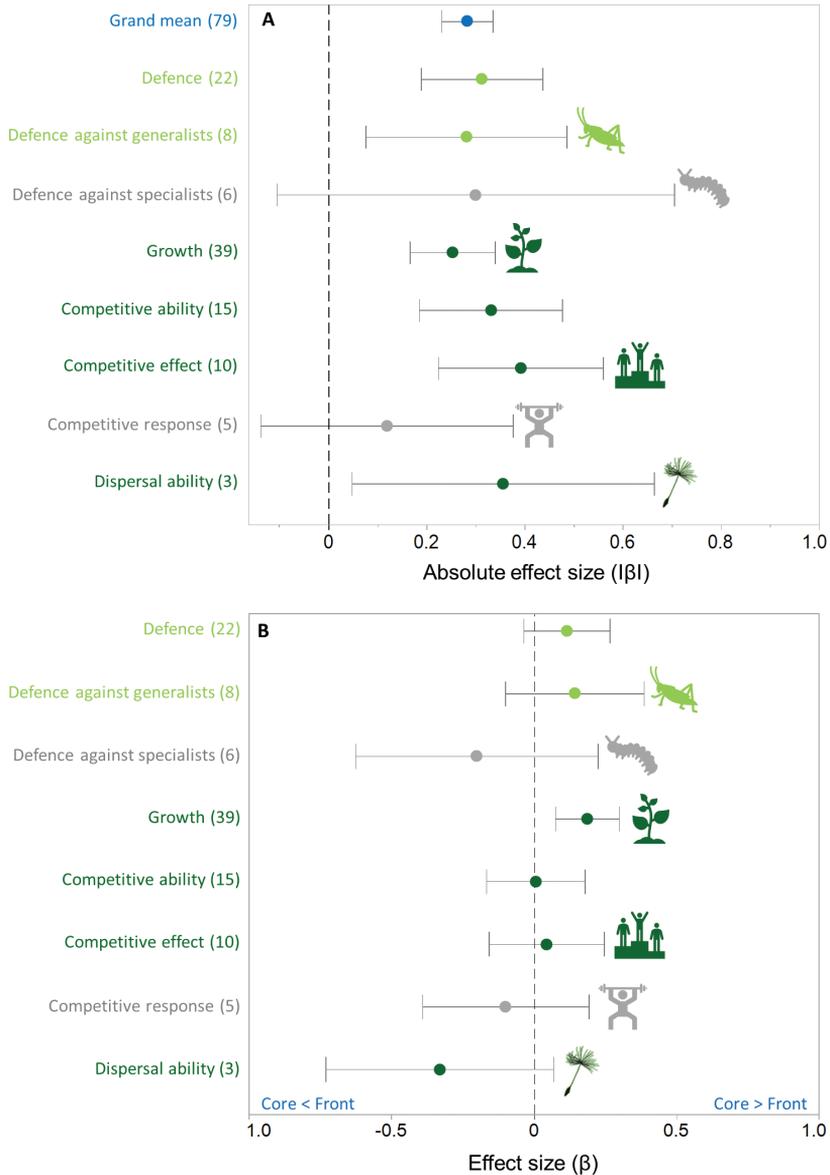


Figure 2. Meta-analysis results showing **A** mean absolute effect sizes ($|\beta| \pm 95\%$ confidence intervals; $0 \leq |\beta| \leq 1$) of differences along invasion history gradients for the grand mean for all categories (blue) and each trait category separately and **B** mean effect sizes ($\beta \pm 95\%$ confidence intervals; $-1 \leq \beta \leq 1$) of differences along invasion history gradients for each trait category. Mean effect sizes are significantly different from zeroes if the confidence intervals do not include zero values, indicating significant trait changes. Negative effect sizes in **B** indicate a negative slope of decreased trait values away from core populations, while positive values indicate an increase towards core populations. Trait categories in light green, dark green and grey, indicate predicted positive, negative or no effect, respectively (see Fig. 1). Sample sizes (number of cases) are indicated in parentheses.

Publication bias

The chosen studies were published between the years 1994–2022. When testing for temporal bias, publication year had no effect on absolute effect size (LMM results: slope \pm SE = 0.0038 ± 0.0058 , $p = 0.51$). Nevertheless, a significant effect of the journal's impact factor was found on absolute effect size, according to which studies with *lower* absolute effect sizes were published in higher impact journals (LMM results: slope \pm SE = -0.039 ± 0.017 , $p = 0.039$; Suppl. material 1: fig. S4A). Moreover, a positive correlation was found between the journal's impact factor and the study's total sample size (Pearson's correlation (log-log scale): $r = 0.539$, $p < 0.001$; Suppl. material 1: fig. S4B). In addition, when time/distance ranges per study was considered, no significant effect of differences in ranges on absolute effect size was observed (LMM results (log range): slope (\pm SE) = 0.036 ± 0.076 , $p = 0.63$). Finally, the estimated Rosenberg's fail-safe number (i.e. additional number of studies with an average effect size of 0 needed to reduce the significance level of the observed average effect size to $\alpha = 0.05$) was 4767, suggesting our results of overall absolute effect size are robust against possible publication bias.

Discussion

Our meta-analysis results reveal overall divergence in invasion-promoting traits with residence time. This divergence was exhibited for all traits, except for competitive response and defence against specialists, which could be attributed to the lower sample sizes of studies that examined these traits in the meta-analysis. However, both our review and meta-analysis results show that, for most studied traits, their divergence lacks a consistent direction.

The only trait for which our meta-analysis revealed a directional shift was plant growth. However, in contrast with our prediction, growth-related traits, such as height and vegetative biomass, increased over time. Invasive plants in older and more established populations were predicted to undergo selection for decreased allocation to growth and competitive ability compared to populations at the invasion front, due an increase in herbivore and pathogen pressure and an allocation trade-off with defence traits. However, of the seven studies explored in our review, only two studies, conducted with the same species (*Lonicera japonica*), provide support for this prediction (Evans et al. 2013; Kilkenny and Galloway 2013). An increased allocation to size in older and more established populations might be driven by increased competition pressure. Specifically, plants in these populations might experience shifts from interspecific competition with diverse neighbours to intraspecific competition with neighbours of similar resource requirements (Lankau et al. 2009; Inderjit et al. 2011), which might be stronger and require greater allocation to growth (Huang et al. 2021). However, the increase in growth with residence time did not translate to increased competitive ability in the meta-analysis results, which might be attributed to the fact that most invasion history studies tested for inter- rather than intraspecific competition (but see Huang

and Peng (2016); Harms and Walter (2021)). Studies that compare competitive ability with heterospecific vs. conspecific neighbours across invasion history gradients are, thus, needed to examine this hypothesis.

The lack of significant consistent directional divergence in most of the traits tested in our meta-analysis could be attributed to varying selection pressures that might be context-dependent and vary with habitat type and resilience of the native communities. Moreover, some gradients of invasion history might take place along geographical gradients, where variation in invasion history could be confounded with other factors, such as changes in ambient temperatures, season length and primary productivity across sites, which could affect the observed patterns (Colautti et al. 2010; Colautti and Barrett 2013; Liu et al. 2017; Hulme and Bernard-Verdier 2018; Irimia et al. 2019; Hierro et al. 2020; Kühn et al. 2021). Several studies have shown that local climates can play an important role in the rapid adaptation of invasive plants and their range expansion (Colautti and Barrett 2013; Vandepitte et al. 2014; Colomer-Ventura et al. 2015; van Boheemen et al. 2019; Haider et al. 2022). For example, Colautti et al. (2009) analysed data from experiments that examined trait divergence of invasive plant species from native and introduced populations and showed that such divergence is highly affected by geographic clines. While we incorporated climatic factors in the analyses whenever available, this was not the case for most of the chosen studies. If such climatic variables can result in divergence in invasion-promoting traits, they may confound divergence due to invasion history. In addition, the evolution of invasive populations might be affected by additional factors whose strength might change with time. For example, as suggested above, while selection pressures that promote greater plant size and competitive ability, such as enemy release, could attenuate with time since introduction, strong competitive ability might still be selected for in older populations if the effect of intraspecific competition is much stronger than that of native heterospecifics.

In addition to different context-dependent selection pressures, the lack of consistent directional change with time since introduction can be attributed to neutral non-adaptive evolutionary processes that might have taken place within the introduced range of some invasive species, such as founder effects and genetic drift. For example, multiple introductions could involve different samplings from the native range, resulting in repeated founder effects of populations with different invasion histories (Parker et al. 2003; Kliber and Eckert 2005; Dlugosch and Parker 2008; Keller et al. 2009). Similarly, successive founder events along invasion routes can result in non-adaptive (or even mal-adaptive) differentiation (Amsellem et al. 2000; Colautti and Lau 2016). In order to discern between evolution due to selection vs. neutral processes along gradients of invasion history, further studies should, therefore, use genetic information of these populations and/or employ reciprocal transplant experiments that test for local adaptations along such gradients (Colautti and Barrett 2013; Moran and Alexander 2014; VanWallendael et al. 2018).

Another explanation for a lack of directional effects of residence time found in this meta-analysis is that, unlike our predictions, trait evolution might follow a non-linear trajectory. For example, recently established populations at the invasion front might

exhibit initial lags in their responses to selection pressures if they are derived from different source populations of different ages or due to factors such as small population sizes. Moreover, evolution of core populations might decelerate if the intensity of selective pressures they experience, such as herbivore load, attenuate with time (Hawkes 2007; Gruntman et al. 2017).

Finally, the lack of a clear directional change might result from the small number of studies on the subject in some of the categories. This is particularly true for traits related to dispersal ability for which we were able to find only three studies that compared dispersal ability across different populations in the introduced range that used common garden experiments. Several other studies have examined the effect of residence time on dispersal ability under field conditions, providing support for such divergence (Tabassum and Leishman 2018; Robinson et al. 2023). However, additional studies that incorporate the effect of residence time on this trait under common garden conditions could provide valuable information and expand the empirical basis and knowledge on its impact on the evolution of invasive plants.

In this review and meta-analysis, we looked at four main categories of invasion-promoting traits for which temporal changes are predicted within the introduced range, including defence, growth, competitive ability and dispersal ability. Yet, additional traits that could contribute to the invasive success of plants might be affected by time since introduction. For example, phenotypic plasticity has been suggested to evolve at the introduced range and facilitate plant invasion in varying habitats and climates (Richards et al. 2006; Davidson et al. 2011). Similarly, selection pressures that might favour phenotypic plasticity are likely to be stronger at the invasion front, where invasive plants encounter novel environmental conditions (Richards et al. 2006; Matesanz et al. 2010). However, while several studies have examined changes in plasticity in response to range shifts (Matesanz et al. 2010), only very few looked at such changes in plasticity along gradients of invasion history (VanWallerdael et al. 2018; Wan et al. 2018).

Conclusions

Adding a temporal dimension to studies on traits of invasive plants is challenging because it entails knowledge on the timing of population establishment or distance to known core populations. However, the potential for rapid evolution of invasive plants within their introduced range across different invasion stages provides a unique opportunity to study fundamental questions related to adaptive divergence in plant traits. Here, we reviewed several hypotheses regarding divergence in invasion-promoting traits, which propose that the effect of varying selection pressures might attenuate with time since introduction. However, while our meta-analysis results reveal a general indication for the evolution of invasive plants with residence time, they do not provide support for a consistent directional divergence, except for growth. Here and in contrast with our prediction, growth parameters were found to increase with invasion history, which might reflect greater competition pressure in these populations.

The general temporal effect found in this study highlights the need to take into account the potential confounding effect of population age when sampling populations to explore attributes of invasive plants (e.g. comparing trait evolution between native and invasive ranges) and particularly when evaluating the long-term effects of invasive plants on native communities and ecosystems. Moreover, the increased size of invasive plants in older populations found in this study, suggests that, although some selection pressures that drive the evolution of invasiveness, such as enemy release, can decrease with time, their dominance and effects on the native communities and ecosystems in the introduced range might not attenuate. Studies that further explore both trait divergence and community effects across invasion routes in the introduced range will be crucial for understanding the long-term dynamics between invasive plants and their recipient native communities.

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Supplementary material I

Supplementary information

Authors: Michal Gruntman, Udi Segev

Data type: docx

Explanation note: **fig. S1.** Temporal trends (between 1977–2022) in studies focusing on exploring variation in invasion-promoting traits of invasive plants over time. Data was extracted after searching the Web of Science Core Collection database using the search terms (chronosequence OR time-since-introduction OR invasion-history OR residence-time OR range-expansion OR colonization-history OR introduction-history) and plant* and invasi* and (biomass OR defense OR competi* OR dispersal OR allelopathy OR herbivor* OR plant-height). The smooth curve (indicated in blue) was added for visual interpretation. **fig. S2.** Schematic representation of the two literature searches used in the meta-analysis, using both Web of Science and Google Scholar databases. **fig. S3.** Meta regression results for the effects of the different moderators on mean absolute effect sizes ($|\beta| \pm 95\%$ confidence intervals; $0 \leq |\beta| \leq 1$). Moderators include the origin of information (invasion history data reported in papers vs. estimated using external databases) and type of invasion history measurement (residence time vs. distance). Sample sizes (number of cases) are indicated in parentheses. **fig. S4.** Correlations between (A) absolute effect size of the different studies and the impact factor of the journal at time of publication or between (B) journal's impact factor and total sample size per study. Dashed lines indicate significant negative correlations ($r = -0.357$, $p = 0.0017$, $n = 75$ and $r = 0.539$, $p < 0.001$, $n = 75$, respectively). **table S1.** Information on the invasive species, variables and factors used for the meta-analysis, as well as the respective effect sizes and variances.

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