



# Re-focusing sampling, design and experimental methods to assess rapid evolution by non-native plant species

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Received: 30 May 2023 / Accepted: 8 January 2024  
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**Abstract** Evolution can occur over contemporary timescales, which may be crucial for the invasive success of non-native plant species. Many studies have shown rapid evolution by comparing native and non-native populations in common gardens. However, our understanding of the mechanisms underpinning rapid evolution is still incomplete. Here, we identify the progress, applications, and limitations of studies on rapid evolution of non-native plants with respect to sampling, experimental design and experimental methods. To encompass broad variation within and between the ranges, we recommend sampling across large-scale environmental gradients. We also

suggest careful consideration of pitfalls related to the choice of seed families and of the biotic interaction under focus. The latter should be chosen with a view on both the experimental treatment and the corresponding field data to estimate population history. Furthermore, we suggest exploiting multiple omics approaches to address the complexity of biotic interactions, and to account for non-adaptive evolution with molecular data on demographic history of populations. We also reviewed papers that studied rapid evolution in non-native plants and quantified how many of these met our criteria. We anticipate that disentangling adaptive and non-adaptive drivers of among-population variation can increase the accuracy of research on rapid evolution, and that integrating phenotypic, metabolomic and population genomic data can bring opportunities for studying complex

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**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10530-024-03249-x>.

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biotic interactions. We also illustrate the importance of large collaborative networks and present our scientific network iCONNECT (integrative CONyza NETwork for Contemporary Trait evolution), with the goal of motivating similar studies on the mechanistic understanding of rapid evolution.

**Keywords** Among-population variation · Biological invasions · Biotic interactions · *Conyza canadensis* · Population history · Rapid evolution

## Introduction

Natural selection can act on very short ecological scales, shifting the genomes, metabolomes and phenotypes of populations over a few generations, a process which is called “rapid evolution” (e.g., Thompson 1998) or in some other contexts also “contemporary evolution” (e.g., Hendry and Kinnison 1999). We here follow the definition of Thompson (1998) using the term rapid evolution as an adaptive process that has immediate ecological consequences on very short evolutionary scales. Rapid evolution can result from standing genetic variation (e.g., altering genotype frequencies through lineage sorting) and from the emergence of novel genotypes, either through recombination within populations or through admixture of previously isolated gene pools (Turcotte et al. 2011; Cameron et al. 2013; Dlugosch et al. 2016). The ability to rapidly adapt to environmental change is of major importance for plant population survival under global change (Hoffmann and Sgrò 2011; Franks et al. 2014; Rosche et al. 2018a; Rauschkolb et al. 2022) and for successful range expansion by non-native plant species (Ochocki and Miller 2017; Szűcs et al. 2017; Woods and Sultan 2022).

Here we focus on rapid evolution in the course of plant invasions. This may happen when non-native plant populations rapidly adapt to novel environmental conditions in their non-native ranges. Many plant invasions are characterized by a “lag-phase”, i.e., delay between the introduction of a non-native species and its successful colonization in a new area (Osunkoya et al. 2021). This process likely coincides with rapid adaptation to the novel environment and is often followed by the colonization of the invader (Aikio et al. 2010; Clements and DiTommaso 2011).

Indeed, many studies have shown genomic, metabolomic and phenotypic differences between native and non-native populations under common garden conditions, indicating rapid evolution as a common occurrence in biological invasions reviewed by Bossdorf et al. (2005); Colautti and Lau (2016); van Kleunen et al. (2018); Clements and Jones (2021). In many cases, rapid evolution was associated with higher performance or greater competitive ability of non-native compared to native populations in common gardens, especially for successful invaders (e.g., Zheng et al. 2015; Montesinos et al. 2019).

There are two reasons why rapid evolution is frequent in biological invasions. First, non-native populations undergo dramatic demographic changes. In particular, population genetic studies often observe colonization bottlenecks or founder effects associated with genetic drift on the one hand and multiple introductions that intensify gene pool admixture on the other hand. Together, these processes can lead to fission and fusion of native gene pools in the non-native ranges (Rius and Darling 2014; Estoup et al. 2016; Rosche et al. 2016). Alexander et al. (2009), for example, showed that population genetic structure was much weaker in the introduced area, and populations were not isolated by distance. Second, such rearrangements of gene pools occur when non-native populations experience fundamentally altered selection pressures as compared to populations in the native range (van Kleunen et al. 2018). Shifts in biotic interactions are considered as the most important selection pressures of rapid evolution in non-native ranges (Moran and Alexander 2014; Dlugosch et al. 2016; Moles et al. 2022; Sheng et al. 2022). The most prominent example in this context may be the release from specialized herbivores and pathogens present in their native ranges (enemy release hypothesis, Keane and Crawley 2002).

In recent years, several hypotheses have been proposed regarding the underlying mechanisms of rapid evolution reviewed by Jeschke and Heger (2018). These hypotheses have been tested in numerous case studies and have significantly improved our understanding of the importance of biotic interactions in biological invasions (Dlugosch et al. 2016). However, studies of rapid evolution are not always carefully set up with rigorous methodologies and there are many contradictory findings when testing theories based on rapid evolution

(Colautti and Lau 2016), including, for example, the “evolution of increased competitive ability-hypothesis” (EICA, Blossey and Notzold 1995; Rotter and Holeski 2018; Callaway et al. 2022).

Because comprehensive frameworks are essential to elucidate the intricacies of adaptive processes over short evolutionary scales, many recent research calls for more sophisticated eco-evolutionary frameworks to study rapid evolution (e.g., Colautti and Lau 2016; Schrieber and Lachmuth 2017; Schrieber et al. 2017; Rotter and Holeski 2018; Rosche et al. 2018b, 2019; Sheng et al. 2022). They identified manifold issues that may arise when studying rapid evolution in biotic interaction traits. First, the samplings in the native and the non-native ranges can be unbalanced, thereby not representing the full breadth of conditions in either range (Colautti and Lau 2016). Second, the experimental set-ups are diverse and each set up comes with its own specific limitations (de Villemereuil et al. 2016; Schrieber and Lachmuth 2017). Third, biotic interactions are complex by nature and therefore difficult to describe and quantify (e.g., competitive ability), making their assessment as selective forces a challenging task for evolutionary ecologists (Aschehoug et al. 2016).

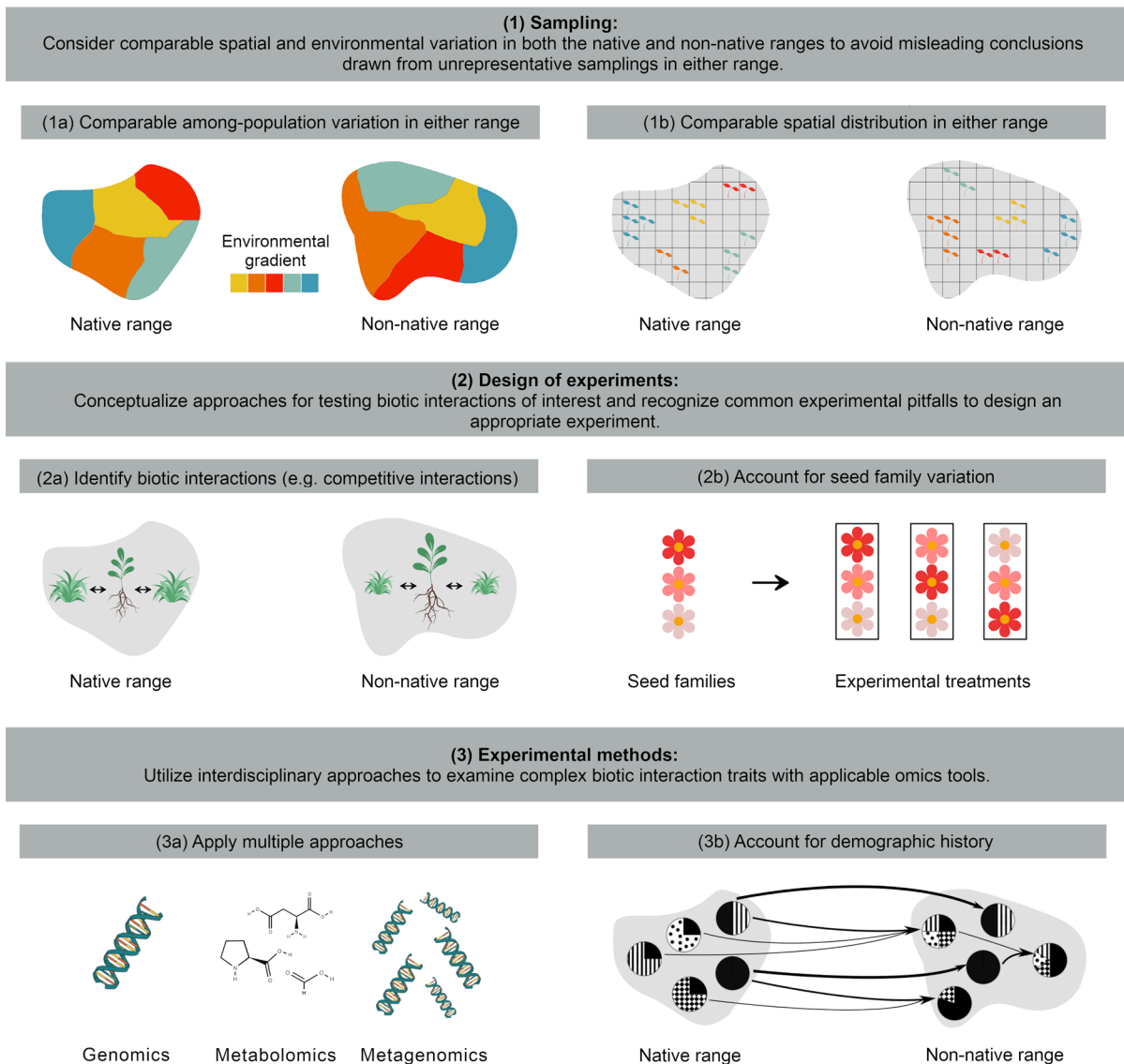
To address apparent issues in studying rapid evolution, we review progress, applications and limitations of current research. Different empirical methods are applied to study rapid evolution from the genetic to the phenotypic levels. Some experiments observe phenotypic shifts under different treatments over a few generations (Williams et al. 2016; Szűcs et al. 2017) whereas others use resequencing approaches to identify allele frequency shifts (Turner et al. 2011; Schlötterer et al. 2015). Also, herbarium specimens can identify trait shifts through invasion histories (Wu and Colautti 2022) and resurrection approaches are used to compare revived ancestors from stored propagules with their progeny (Sultan et al. 2013; Franks et al. 2018; Rauschkolb et al. 2022). However, we focus here on classical population ecological studies which represent the vast majority of studies dealing with rapid evolution, i.e., experimental setups that compare native and non-native populations under common garden conditions. In this context, we focus on three topics where we believe progress is needed to advance our mechanistic understanding of rapid evolution (Fig. 1):

- (1) *Sampling* Consider comparable spatial and environmental variation in both the native and non-native ranges to avoid misleading conclusions drawn from unrepresentative samplings in either range.
- (2) *Design of experiments* Conceptualize approaches for testing biotic interactions of interest and recognize common experimental pitfalls to design an appropriate experiment.
- (3) *Experimental methods* Utilize interdisciplinary approaches to examine complex biotic interaction traits with applicable omics tools.

We propose considerations that researchers should make when designing studies that test differences between native and non-native populations. We also reviewed papers from the journal *Biological Invasions* that studied rapid evolution in non-native plants using common garden approaches (Table 1) and quantified how many of these met our criteria (related to the topics 1 to 3 above). Finally, we illustrate the importance of large collaborative networks and present our scientific network iCONNECT (integrative CONyza NETwork for Contemporary Trait evolution) in which we are studying rapid evolution in competitive ability of native and non-native populations of *Conyza canadensis* (syn. *Erigeron canadensis*), as an example of how this could be achieved.

#### Sampling comparable spatial and environmental variation in both ranges

Common garden experiments have frequently found differences between native and non-native populations (Kulmatiski 2019; Montesinos 2022; Zhang et al. 2022). Such between-range differences may suggest evidence for rapid evolution assuming that they are based on altered selection pressures between the ranges. However, between-range variation is just a part of the global spectrum of among-population variation (APV, i.e., intraspecific trait variation that is due to selection pressures associated with population history). In this regard, it is important to consider that populations from both native and non-native ranges can show strong within-range variation in their population history (Oduor et al. 2022; Sheng et al. 2022). This means that the choice of sampled populations from either range can obviously affect the results of



**Fig. 1** Conceptual outline how to overcome current limitations in (1) sampling, (2) experimental design, and (3) experimental methods to study rapid evolution between native and non-native ranges. We suggest (1a) sampling broad and comparable variation in environmental gradients within and comparable variation in environmental gradients within and between native and non-native ranges, (1b) sampling comparable spatial distribution in either range, (2a) evaluating the focal biotic interaction for both the design of experimental treat-

ments and the collection of field data on population history. Experiments should also consider (2b) pitfalls related to seed family selection. In addition, we propose to use multiple omics approaches to (3a) capture the complexity of biotic interactions with currently available tools and to (3b) account for non-adaptive evolution with molecular data on population demographic history

native vs. non-native comparisons in the common garden (Rosche et al. 2018b, 2019).

Colautti and Lau (2016) reviewed 31 studies that postulated rapid evolution in non-native populations. They used data simulations and found that 24 of these

studies did not present sufficient data to support their conclusions. Most of them compared only few and rather haphazardly chosen populations from large areas and therefore underestimated APV within each range. Many studies also sampled along different

**Table 1** Papers from the journal Biological Invasions that studied rapid evolution in non-native plants using common garden approaches

Study	Objective	Populations involved	Met suggestions
Shi et al. (2023)	Analyze plant chemistry of F1-offspring of within-population and between-population crosses using metabolomics	3 native and 3 non-native <i>Lythrum salicaria</i> populations	2a
Hoffbeck and TerHorst (2022)	Quantify differences in life history traits between and within native and non-native ranges, among and between genotypes	10 native and 10 non-native <i>Medicago polymorpha</i> populations	None
Ferrero et al. (2020)	Quantify geographical variation among ranges, regions and populations in traits and ploidy level	33 native and 110 non-native <i>Oxalis pes-caprae</i> populations	1a,2b
Hernández et al. (2019)	Test for rapid adaptive evolution of seed traits in response to novel abiotic conditions	15 native and 7 non-native <i>Helianthus annuus</i> populations	None
Irimia et al. (2019)	Test biogeographical differences in allelopathic effects	10 native and 20 non-native <i>Centaurea solstitialis</i> populations	1a,2b
Luo et al. (2019)	Compare differences in phenotypic traits and in their plasticity between populations subjected to high and low nutrient availability	3 native and 3 non-native <i>Plantago virginica</i> populations	2b
Montesinos et al. (2019)	Examine competitive responses and competitive effects across ranges	8 native and 8 non-native <i>Centaurea solstitialis</i> populations and 8 native and 8 non-native <i>C. calcitrapa</i> populations	2b
Peng et al. (2019)	Understand how climate warming and atmospheric nitrogen deposition influence are related to fitness	1 native and 1 non-native <i>Solidago canadensis</i> populations	None
Tavares et al. (2019)	Test genetically based phenotypic differences regarding competitive ability	23 native and 12 non-native <i>Oxalis pes-caprae</i> populations	1a
Turner et al. (2017)	Investigate gene expression during drought response that might underlie variation in drought tolerance	3 native and 3 non-native <i>Centaurea diffusa</i> populations	None
Guo et al. (2016)	Assess the differentiation in phenotypic traits between genotypes and see if can be explained by contrasting habitats and climatic conditions	4 native and 4 non-native <i>Phragmites australis</i> populations	None
Vandegrift et al. (2015)	Test whether founder effects or other evolutionary forces are related to enemy release and the EICA hypotheses	10 native and 6 non-native <i>Brachypodium sylvaticum</i> populations	2a
Mimura et al. (2013)	Compare phenotypic and genetic variation among genotypes to investigate the source and role of standing variation	11 native, 7 non-native and 4 cultivars <i>Lotus corniculatus</i> populations	2b
Eriksen et al. (2012)	Identify candidate morphological and life history traits that may have been influenced by natural selection and contributed to fitness and adaptation	2 native and 2 non-native <i>Centaurea solstitialis</i> populations	None
Qing et al. (2012)	Test for evolutionary change between ranges with respect to nitrogen allocations between cell walls and photosynthetic proteins	3 native and 3 non-native <i>Spartina alterniflora</i> populations	None

**Table 1** (continued)

Study	Objective	Populations involved	Met suggestions
Erfmeier and Bruelheide (2010)	Assess nutrient supply, temperature and community characteristics and quantify the environmental pressure in native and non-native ranges	12 native and 6 non-native <i>Rhododendron ponticum</i> populations	None
He et al. (2010)	Compare the total biomass and phenotypic plasticity indices under stressed and non-stressed conditions	18 native and 13 non-native <i>Centaurea stoebe</i> populations	1a

The selected papers were checked with respect to the criteria suggested in Fig. 1 on sampling (1a. comparable APV range, 1b. comparable spatial distribution), design of experiments (2a. biotic interactions, 2b. seed family variation), and experimental methods (3a. multiple approaches, 3b. demographic history). Details on the study selection and on the evaluation whether the studies met the suggestions can be found in the Supporting Information.

environmental gradients in the native vs. non-native ranges. We found that only 23.5% of our reviewed studies sampled native and non-native populations across comparable environmental gradients in either range. In those cases, significant differences between native and non-native populations might result from within-range APV, which was not measured in both ranges to a comparable extent (Rosche et al. 2019). To ensure appropriate between-range comparisons testing for rapid evolution, studies should have sufficient and representative environmental variation in both the native and non-native ranges (Fig. 1-1a). This can be achieved by sampling as many populations as possible while maximizing environmental variation in both ranges. Another solution was recently demonstrated by Sheng et al. (2022) who paired four matching bioclimatic regions in the native and non-native ranges to have comparable climatic backgrounds for their study populations from either range.

Besides incorporating environmental gradients in the sampling design, studies should also sample comparable spatial distributions in native vs. non-native ranges (Fig. 1-1b). We found that none of our reviewed studies sampled native and non-native populations along comparable spatial distances in either range. This is important because variables measured from locations close to each other often exhibit more similar values than those from further apart (i.e., spatial autocorrelation, Legendre 1993). A regional clustering of samplings can help to account for spatial auto-correlation if number and spatial distances of populations within geographical regions are comparable among the regions and between native and non-native ranges (Sheng et al. 2022). Such sampling design may allow setting population nested

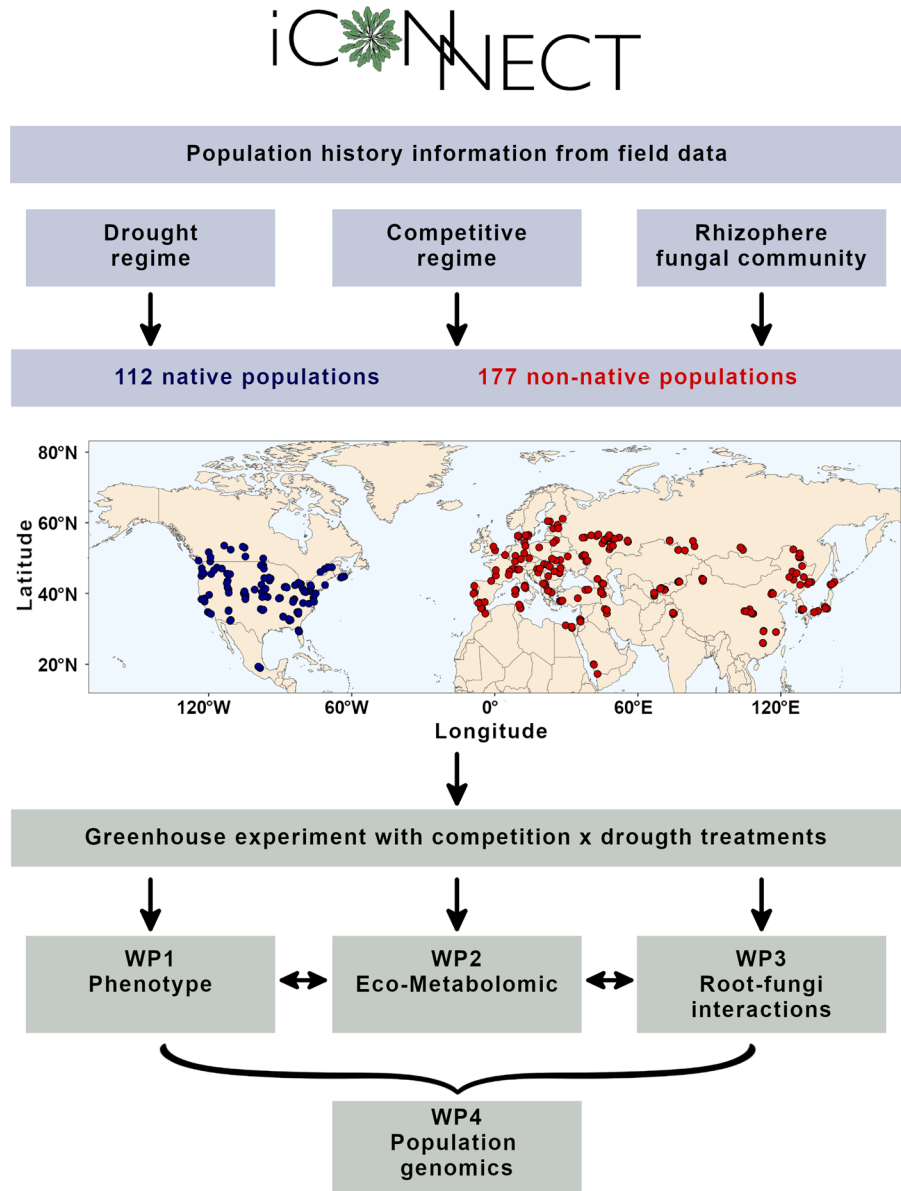
within region as a random effect which was recently shown to appropriately account for spatial auto-correlation in native vs. non-native range comparisons (Rosche et al. 2019). There are many other statistical approaches that account for spatial auto-correlation in ecology but all of which benefit from a judicious representation of spatial distributions (see Kuehn and Dormann 2012).

#### Conceptual approaches for experimental designs

To investigate the degree to which differences between native and non-native populations are attributable to rapid evolution, rather than other components of APV, it is important to identify biotic interactions (Fig. 1-2a) that differ between the ranges with the potential to alter selection pressures (Jones and Gomulkiewicz 2012; van Kleunen et al. 2018). There are many types of biotic interactions that determine the success of invasive species, such as pollination (Harmon-Threatt et al. 2009; Mackin et al. 2021), herbivory (Hu and Dong 2019; Yin et al. 2023), pathogen infestation (Goss et al. 2020), soil biota mutualisms (Callaway and Lucero 2020; Sheng et al. 2022) and competitive interactions (Shah et al. 2014). For the sake of clarity, we here focus exemplarily on competitive interactions, but our descriptions arguments below can be applied in a similar way to other biotic interactions under focus.

Competitive interactions are among the most important biotic interactions that determine the success of invasions (Callaway et al. 2011) because native and non-native species often interact differently with co-existing species (Felker-Quinn et al. 2013; Shah et al. 2014; Pearse et al. 2019; Pal et al.

**Fig. 2** Conceptual scheme of the current research in the iCONNECT project that aims to disentangle drivers of rapid evolution in the competitive ability of *Conyza canadensis*. The project has four connected and interdisciplinary work packages (WPs) that analyze data from one greenhouse experiment (olive boxes). The experiment investigates among-population variation in the response of 112 native and 177 non-native populations to experimental competition  $\times$  drought treatments. Available field data will be used as a proxy for the population history of the local drought regime, the competitive regime, mutualist-pathogen ratio in the field rhizosphere (gray boxes). The population history data and data on neutral genetic relatedness of the populations are anticipated to help disentangling how adaptive and non-adaptive evolution determinants drive among population variation with respect to the response to experimental competition  $\times$  drought treatments, both within and between native and non-native ranges



2020; Nagy et al. 2022). Studies on rapid evolution often select treatments that simulate the particular biotic interaction assumed to drive rapid evolution (e.g., Turcotte et al. 2011; Schrieber et al. 2017; Macel et al. 2017; Rosche et al. 2018b; Javed et al. 2020). For example, if different competitive interactions between the native and non-native ranges are observed in the field, studies can apply a competition treatment under common conditions (e.g., neighbor vs. no neighbor; e.g., Shah et al. 2014). Such a design allows recording whether the response to the

experimental treatment differs between the ranges (i.e., range  $\times$  treatment interaction).

To integrate the effects of APV within and between ranges, field data that deal with the biotic interaction of interest can be included in the models as a proxy for population history. Such proxies can explicitly test whether the strength and direction of natural selection in recent population history differ between native and non-native ranges (i.e., range  $\times$  population history  $\times$  treatment interaction; e.g., Schrieber et al. 2017; Rosche et al. 2018b; Vilellas et al. 2021).

Moreover, such assessments allow testing for differential effects of plasticity vs. local adaptation in both native and non-native ranges (Villellas et al. 2021). In studies of competition as the main driver of rapid evolution, field data on the competitive regime can be used to test whether competition in the population history has the same effects on competitive ability in the greenhouse in native vs. non-native populations (Lachmuth et al. 2011; Heger et al. 2014). As an example different from competitive interactions, Schrieber et al. (2017) investigated how the herbivory that native and non-native populations experienced in the field affected experimental herbivory under common garden conditions. However, only 11.8% of the reviewed studies investigated how biotic interactions experienced in the field might affect the outcome of corresponding experimental treatments as an indication of rapid evolution.

Another important point for designing experiments is the consideration of seed family variation to minimize unexplained variance in common garden experiments (Fig. 1-2b). Within populations, genotypes may differ in phenotype with some genotypes showing a high performance across multiple environments (e.g., general purpose genotype, Barrett 2016), which can be a problem for experimental designs. For example, in competition experiments, an overrepresentation of general purpose genotypes in the “competition treatment” as compared to the “no competition treatment” may lead to overestimation of the population’s competitive ability. One way to avoid this pitfall is to control for equal distribution of seed families across the experimental treatments in the greenhouse (Lachmuth et al. 2011; Schrieber et al. 2017). 29.4% of the papers that we reviewed used different seed families in their experiments to distribute them equally across their treatments. This means that the effect of individual genomes has been underestimated in the majority of the studies.

Other considerations in experimental design regarding the seed families include maternal effects and breeding background (Pico et al. 2003). Offspring may show responses to conditions experienced by the mother (maternal effects, Herman and Sultan 2011; Heger 2016). Moreover, field conditions influence the resource availability of the mother plant and thus indirectly affect the offspring in the experiment (Veselá et al. 2021). Greenhouse estimates of population fitness thus depend on the environmental conditions

that the mothers faced in the sampling year (de Villemereuil et al. 2016; de Kort et al. 2020). Differences in mother fitness on offspring performance may be accounted for by including seed mass as a covariate in the models (Dyer et al. 2010). Also, the breeding background of an individual (e.g., selfing, biparental inbreeding, outcrossing) can affect its performance (reviewed by Angeloni et al. 2011). This may result in unexplained variance in experiments on rapid evolution (Rosche et al. 2017; Schrieber et al. 2017; Gustafsson et al. 2022). The use of F1-offspring generated under standardized environmental and breeding conditions can control for both maternal effects and breeding background. However, such approach would reduce epigenetic variation which—depending on the research question—can be preferable or not.

#### Experimental methods: utilizing various omics approaches

Traditionally recorded phenotypic data can only provide inference of rapid evolution and ideally should be accompanied by molecular data (de Villemereuil et al. 2016, 2022). However, most native vs. non-native range comparisons have focused on phenotypic data reviewed by Bossdorf et al. (2005). Others have used population genomic reviewed by Flucher et al. (2021), or metabolomic data (e.g., Macel et al. 2014; Wu et al. 2020; Yu et al. 2022; Yin et al. 2023), but these did not cover APV in both ranges. In fact, studies that cover both molecular and phenotypic data across broad spatio-environmental gradients are rare and almost exclusively focus on *Arabidopsis thaliana* (e.g., Mönchgesang et al. 2016; Exposito-Alonso et al. 2019). In our review, none of the studies used multi-omic approaches. This is an important knowledge gap as complex biological questions cannot be investigated using only a few genotypes or populations (Des Roches et al. 2018; Milcu et al. 2018). With insights into drivers of rapid evolution in biotic interactions, applying multiple omics approaches may be particularly promising (Fig. 1-3a) because biotic interactions are often characterized by trait complexes which are difficult to understand, quantify, or even to define. For example, competitive ability is a complex of traits comprising the tolerance of an individual to the suppressive effects of nearby plants, and traits that usurp resources from a finite pool and traits that



directly inhibit growth of neighboring plants (Aschehoug et al. 2016).

### Molecular interaction ecology

Eco-metabolomics is a powerful tool for understanding the underlying mechanisms of ecological processes (Peters and Worrlich 2018), may help to understand hitherto unexplained variation in plant interactions (Walker et al. 2022; 2023) and can unravel strategies of invasive plants (Macel et al. 2014). Metabolites are viewed as one of the intermediary layers between the genome and expressed phenotypes, and thus represent a key component to understanding how species interact (Yang et al. 2021; Walker et al. 2022; Auwerx et al. 2023). We here focus exemplarily on studying root exudates; yet, metabolomics can be applied for studying many other biotic interactions (e.g., studying secondary metabolites in leaves in herbivory studies, Wu et al. 2022).

Root exudates can have direct effects on the competitive ability of plants via the toxic suppression of nearby plant growth, known as allelopathy (Semchenko et al. 2014). The novel-weapons hypothesis posits that the overwhelming success of some plants in their non-native ranges is due to allelopathic suppression of native species that are not adapted to the novel chemical traits (Hierro and Callaway 2021). At the same time, an increased allelopathic susceptibility of local competitors in non-native ranges may stimulate rapid evolution for the production of allelopathic substances between native and non-native ranges, although this has rarely been investigated (but see Irimia et al. 2019 for leaf leachates). Moreover, root exudates may shape the soil biota community in the rhizosphere by attracting mutualists or repelling pathogens (Weidenhamer and Callaway 2010; van Dam and Bouwmeester 2016; Yu et al. 2022). This is important because shifts in soil biota communities affect resource availability and can have strong indirect effects on competitive interactions among plants, while these relationships may differ strongly in native vs. nonnative ranges (Lekberg et al. 2018).

Many studies support enemy release from soil biota in non-native ranges, particularly for specialized pathogens (Kulmatiski et al. 2008; Flory et al. 2011). The reduced pathogen pressure in non-native populations may also facilitate beneficial interactions with mutualists (Reinhart and Callaway 2006; Sheng

et al. 2022). This aligns with competition experiments where non-native plants benefit more than native plants from the presence of soil fungi (e.g., Callaway and Lucero 2020). However, while the evolutionary consequences of biotic interactions have been studied extensively for aboveground interactions, we know very little on how altered soil biota communities may trigger rapid evolution in non-native plants (Lekberg et al. 2018; Sheng et al. 2022). Current meta-genomic tools such as next generation amplicon sequencing or the recent progress in analyzing root exudates increase our abilities to address such questions related to the “belowground black box” (van Kleunen et al. 2018).

### Population genomics and rapid evolution

High throughput sequencing approaches are revolutionizing the field of eco-evolutionary genomics by providing large amounts of genome-wide single nucleotide polymorphisms (SNPs, Andrews et al. 2016). The availability of thousands of SNPs facilitates our ability to unravel how gene flow is controlled by the interplay of adaptive vs. non-adaptive drivers of the dispersal probability at the global scale (Orsini et al. 2013; Levy and Boone 2019). Quantifying gene flow among populations is crucial for a comprehensive understanding of the demographic history of populations (Fig. 1-3b, Al-Gharaibeh et al. 2017; Nagy et al. 2018; Vendrami et al. 2019; Walsh et al. 2021), and important for predicting native source populations and reconstructing the invasion history of non-native populations (Fitzpatrick et al. 2012; Hou and Li 2020; Bieker et al. 2022; Encinas-Viso et al. 2022; McCulloch et al. 2023).

Moreover, knowledge on the demographic history of populations allows accounting for non-adaptive evolution when analysing phenotypic or metabolomic APV (Raeymaekers et al. 2017; de Villemereuil et al. 2022). APV in general, and between-range variation more specifically, is not only caused by natural selection but can also result from purely demographic processes such as genetic drift and migration history (i.e., population co-ancestry, Keller and Taylor 2008). For example, Rosche et al. (2019) used pedigree mixed-effects models that account for population co-ancestry and demonstrated for *C. canadensis* that non-adaptive evolution may false-positively indicate rapid evolution or obscure adaptive effects due to

unexplained residual variance. This variance is particularly useful for studying rapid evolution because both fission and fusion of native gene pools can shift allele frequencies towards sweep scenarios, where adaptive allele frequencies vary greatly across non-native populations without actually corresponding to any selection pressures (Ravinet et al. 2017; Rosche et al. 2019; Irimia et al. 2023). However, our review indicated that none of the studies have taken population genomic information into account to analyses when studying rapid evolution in non-native plants.

Furthermore, mapping high throughput SNP data on assembled genomes can identify genomic regions that are associated with environmental gradients in population histories (McKown et al. 2014). Similarly, these data can detect genomic regions that are associated with phenotypic and metabolomic APV in common garden experiments. Combined, these data provide insights into whether selection patterns in the population history correspond with APV in experiments (Exposito-Alonso et al. 2019). Mapping of candidate SNP loci can also identify functional genes that are potentially related to APV. This may allow, for example, identifying gene size changes, novel genomic rearrangements and local adaptations underpinning rapid evolutionary change (Andrews et al. 2016; Hendry 2016; Rudman et al. 2018), and may also be used to design probes for sequence capture approaches in further studies (Fahrenkrog et al. 2017; Capblancq et al. 2020). Together, these approaches can assess the causality of adaptive correlations observed in eco-evolutionary studies.

#### Large collaborative networks to address adaptive evolution

Large collaborative networks are crucial for advancing our understanding of ecology and evolution (Goring et al. 2014; Papale et al. 2020). Existing networks that address adaptive evolution on global scales include, for example, the Global Urban Evolution Project (GLUE, Santangelo et al. 2022), the PLANTPOPNET (Smith et al. 2020), and the Genomics of Rapid Evolution in Novel Environments-net (Czech et al. 2022). These networks bring together large amounts of data across broad spatio-environmental scales and involve experts from diverse backgrounds, enabling the integration of

various perspectives and methodologies. Together these characteristics address three important issues when studying complex evolutionary questions. First, studying evolutionary ecology requires extensive datasets across many populations and time periods (Vermeulen et al. 2013). Second, biogeographic regions can fundamentally differ in how environmental changes affect adaptation (Exposito-Alonso et al. 2019) and how this affects biotic interactions (Lee et al. 2022). And third, evolutionary biology is inherently interdisciplinary, drawing from genetics, metabolomics, ecology, and other fields (Craven et al. 2019).

Here, we introduce iCONNECT, which is a new large collaborative and interdisciplinary network investigating mechanisms driving rapid evolution in *C. canadensis* (<https://conyzaconnect.wixsite.com/iconnect>). This framework is an open collaboration of researchers who contribute to the sampling of populations from the Northern Hemisphere, and researchers who investigate APV on sampled populations in their particular field. We use *C. canadensis* as a model because it is a successful invader, and an economically significant agricultural weed (Okada et al. 2015). The species is native to large parts of North America and non-native to large parts of the rest of the temperate and subtropical world. This cosmopolitan distribution allows studying APV in biotic interactions across large climatic gradients. *Conyza canadensis* has a high capability for rapid evolution given by that it was the first eudicot weed that evolved glyphosate resistance, independently at multiple locations (Okada et al. 2015).

Our current research investigates the drivers of rapid evolution in the competitive ability of *C. canadensis* under mesic vs. drought-stressed conditions. To do so, we investigate how population history determines APV under common garden conditions for competitive ability, drought responses, root exudate profiles, allelopathic activity, resource acquisition patterns and, interactions with mutualistic and pathogenic fungi (Fig. 2). In addition, correlating data across the interdisciplinary work packages can help to unravel how belowground mechanisms determine competitive ability. This includes genome-wide association studies to identify genomic regions that drive rapid evolution in competitive ability.

## Conclusion

The understanding of rapid evolution is still incomplete despite tremendous efforts that have been made with diverse approaches in common garden studies. There are only few studies on rapid evolution that explicitly disentangle how population history drives APV within and between native and non-native ranges. There is also a lack of interdisciplinary frameworks that could identify the underlying mechanisms of rapid evolution, particularly studies involving multi-omics approaches. In this conceptual paper, we reiterate the call for more sophisticated eco-evolutionary frameworks to study rapid evolution (e.g., Mráz et al. 2014; Schrieber et al. 2017; Rosche et al. 2018b, 2019) by focusing on three topics: (1) sampling, (2) design of experiments, and (3) experimental methods.

We argue that integrating data-intensive research on phenotypes, metabolomics, belowground amplicon sequencing and population genomics offers promising opportunities for studying complex biotic interactions. Considering these aspects, we outline how to study rapid evolution in the context of competitive ability under changing environmental conditions and introduce our scientific network iCONNECT. Our conceptual approach, however, is applicable to other invasive species and other types of biotic interactions and we emphasize the value of large collaborative networks to address such research. We hope that our considerations can be helpful for researchers that design studies on rapid evolution to test for differences between native vs. non-native populations.

**Acknowledgements** We thank Heidi Hirsch for her help in developing the illustrations. We also gratefully acknowledge the financial support of the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) and the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig within the framework of Flexpool. The associate editor and two anonymous reviewers provided very helpful criticisms of earlier versions of the manuscript.

**Author contributions** All authors contributed to the study conception and design. LMS wrote the manuscript with support from CR and IH, and substantial input from all authors. All authors read and approved the final manuscript.

**Funding** Open Access funding enabled and organized by Projekt DEAL. This research was supported by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation; Project project number: RO 6418/1-1) and iDiv Flexpool funding (grant number W47038118). The German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig is

funded by the German Research Foundation (DFG–FZT 118, 202548816).

## Declarations

**Conflict of interest** The authors have no relevant financial or non-financial interests to disclose.

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