



TRAIT EVOLUTION IN INVASIVE SPECIES

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Abstract: One of the most exciting recent developments in the field of invasion biology has been the growing realisation that evolution can determine invasive species' success. Here, we review research on contemporary evolution in invasive populations, with a focus on traits that have the potential to contribute to invasive spread. Evidence available so far indicates adaptive divergence in quantitative traits predominates, although the contribution of non-adaptive processes should not be easily discounted. Further, contemporary evolution of invasive populations appears to be more frequently spurred by abiotic factors, rather than escape from natural enemies. Important progress remains to be made on the role of hybridisation in invasion success, or the conditions under which rapid evolution of phenotypic plasticity at key traits leads to invasions. Also, we do not yet have a firm grasp on how often expansion load limits invasive spread. While convincing examples of adaptation along geographic or climatic gradients are available, we highlight conditions under which such clines would arise irrespective of biotic or abiotic conditions. We propose potentially important future lines of investigation that can illuminate the mechanistic basis of invasion success while maximising the value of invasive species for understanding evolutionary processes.

Keywords: biological invasion, introduction, EICA, adaptation, trait evolution, plasticity, hybridisation, range expansion, dispersal

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1 Introduction

The classical view of evolution by natural selection is that the process is gradual, occurring over millennia. However, studies of contemporary evolution in a wide array of species have overturned this idea (Grant and Grant, 1995; Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Hendry, 2016). Key among these are investigations of rapid evolutionary change in invasive species, where numerous studies have demonstrated that invasion can have large impacts on both adaptive and non-adaptive evolution (Colautti et al., 2009; Dlugosch and Parker, 2008; Colautti and Lau, 2015). Such studies of trait evolution in invasive species have allowed the tempo of contemporary evolution to be quantified (Hendry and Kinnison, 1999; Kinnison and Hendry, 2001; Bone and Farres, 2002) and have furthered understanding of how genetic, demographic, and ecological factors shape rapid evolution. Understanding trait evolution in introduced species is important because it can impact demographic parameters key to invasion success. For example, adaptation can result in evolutionary rescue when a species is introduced to a harsh environment where it is otherwise doomed to extinction (Gomulkiewicz et al., 2010). Accordingly, invasions offer opportunities to explore eco-evolutionary dynamics, whereby evolution during invasion can impact spread and abundance of the invader with consequences for recipient communities. In the following sections, we provide a comprehensive review of trait evolution in invasive species, focusing on the traits that have the potential to contribute to invasive spread.

2 Interspecific Comparisons and the Identification of Invasiveness Traits

The first attempt to characterise traits that determine invasion success is most commonly pegged at 1965, with the publication of *The Genetics of Colonizing Species* (Baker and Stebbins, 1965). In this classic volume, Herbert G. Baker used a series of congeneric comparisons to compile a list of 14 traits that would characterise a hypothetical 'ideal weed' (Baker, 1965). While Baker's definition of a weed was broader, and included colonisers of disturbed habitats, most species considered were invasive (van Kleunen et al., 2015). The list included, among other traits, rapid development to flowering, high seed output, increased competitive ability (e.g. through allelopathy), vigorous vegetative reproduction, and increased phenotypic plasticity. With this list, Baker expanded on his previous work that proposed self-compatibility as a major trait facilitating long-distance colonisation (Baker, 1955). Two aspects of the 'ideal weed' list are important to emphasise. First, Baker recognised that its applicability will vary. For instance, in his 1974

revision of the list, he emphasised that taxa will span the continuum from minor weeds, whose success he attributed to 'fortuitous pre-adaptation', to major weeds, for which evolution has 'compounded [multiple weediness] adaptations' (Baker, 1974). Second, the list was not intended as a rigorous quantitative examination of invasiveness traits but was instead a synthesis of non-experimental case studies (see also Barrett, 2015), performed with the goal of defining a weediness syndrome.

In the following years, a number of studies did not find support for the 'ideal weed' list, and invasion biologists grew increasingly sceptical of the utility of Baker's scheme (Williamson, 1999). Perrins et al. (1992), for example, calculated weediness scores for 49 annual plants in the British flora and related this metric to trait divergence. None of the phenotypes investigated were differentiated between weeds and non-weeds. Results from early attempts were not all contradictory of Baker's view, however. Rejmanek and Richardson (1996), for instance, analysed trait differentiation among 24 introduced *Pinus* species, containing an equal representation of invasive and non-invasive taxa. As expected, invasive species tended to be r-strategists and were characterised by small seeds, as well as early and consistent reproduction (Rejmanek and Richardson, 1996; Rejmanek, 1996).

Recently, interspecific comparisons probing the validity of invasiveness traits have increased in frequency on the backdrop of more comprehensive plant trait databases, expanded regional species inventories, and improved analytical tools. These studies tend to focus on floras of invaded regions (Pysek and Richardson, 2007). Two types of comparisons are performed, producing broadly comparable results: native–alien comparisons and alien–alien comparisons (Pysek and Richardson, 2007; van Kleunen et al., 2010). Native–alien comparisons investigate trait differentiation between local native species and local invasive species. Because these studies consider all invasive taxa in a region to be equivalent, they make the simplifying assumption that the same traits are beneficial across all stages of the invasion process. Evidence available so far indicates that this assumption does not always hold (Kolar and Lodge, 2001; Dawson et al., 2009; van Kleunen et al., 2015). Alien–alien comparisons avoid this by comparing widespread invasive species with co-occurring, but less-successful invasives. Even in this case, however, potential sources of bias remain, such as time since introduction (Hamilton et al., 2005). Lastly, both native–alien and alien–alien comparisons are likely to lead to conflicting results when the spatial scale under investigation differs between studies (e.g. analyses performed at a regional vs. a continental scale; Hamilton et al., 2005).

With these caveats in mind, it is notable that some candidate invasiveness traits have been gaining increased support (reviewed in Pysek and Richardson, 2007). Among morphological traits, plant height, used as an indicator of competitive ability (Dostal, 2011), has often been identified as an outlier in invasive species (Pysek et al., 1995; Williamson and Fitter, 1996;

Moravcova et al., 2015). Note, however, that plant height was not a strong predictor of invasiveness in an analysis of Australian flora that controlled for residence time, phylogenetic relatedness, and the contribution of other traits (Hamilton et al., 2005). Also, in agreement with Baker's predictions, vigorous vegetative reproduction has been confirmed as a good predictor of invasive status (Pysek, 1997; Kolar and Lodge, 2001; Lloret et al., 2005). Among physiological traits, increased specific leaf area, commonly used as an indicator of high resource acquisition capacity and relative growth rate (Reich et al., 1997), has emerged as one of the most reliable predictors of invasiveness (Lake and Lewisham, 2004; Hamilton et al., 2005; Grotkopp and Rejmanek, 2007). Among reproductive traits, consistent support has been obtained for early flowering time and prolonged flowering duration (Pysek et al., 2003; Lake and Lewisham, 2004; Lloret et al., 2005). Results for propagule (seed) size, on the other hand, have been mixed (Pysek and Richardson, 2007), potentially because contrasting seed sizes are favoured at different stages of the invasion (Moodley et al., 2013).

Aside from re-affirming the importance of morphological, physiological, and reproductive traits in the invasion process, these studies have made clear that results are context dependent. Such contexts may be temporal or spatial (Hamilton et al., 2005), reflecting the contribution of evolutionary change and/or phenotypic plasticity. For example, when interspecific native–invasive comparisons are performed under multiple standardised growing conditions, results often point towards higher plasticity of species categorised as invasive (Richards et al., 2006), as initially predicted by Baker (1965). Increased plasticity can facilitate invasions by allowing invasive species to maintain high fitness across a broader range of conditions and/or to more efficiently exploit one end of an environmental gradient (Richards et al., 2006). Evidence accumulated so far from interspecific comparisons indicates the latter scenario is more common, with invasive species typically outperforming native species under non-limiting conditions (Funk, 2008). It is important to emphasise, though, that meta-analytical support for these observations has so far been mixed, with studies both in favour of (Davidson et al., 2011) and opposed to (Palacio-Lopez and Gianoli, 2011) higher plasticity in invasives (for an interpretation of these findings, see Section 3.5).

While, as highlighted earlier, research on invasiveness traits performed at the interspecific level has been highly informative, limitations remain. For one, the majority of studies necessarily focus on the subset of traits that are easily accessible from herbarium records. Oftentimes, data on traits such as growth rate or flowering duration, which may be relevant for invasion success, is not available (Pysek and Richardson, 2007). Also, interspecific comparisons frequently identify a host of differentiated traits or trait categories (van Kleunen et al., 2010). Without investigations of incipient stages of the

invasion process, incorporating comparisons of trait divergence among populations within species, it remains challenging to disentangle the sequential contribution of traits to invasion success. Lastly, the interspecific approach does not provide information on the origin of invasiveness traits, because in this case pre-adaptation cannot be separated from post-introduction evolution. Hereafter, we focus on evidence of trait differentiation within invasive species. We discuss results from comparisons between the native and introduced ranges, or between populations within the introduced range.

3 Between-range Comparisons

3.1 Non-adaptive Trait Divergence Between Native and Introduced Ranges

Biological invasions are sampling events during which a fraction of the diversity present in the native range seeds non-native range expansions. Introduction bottlenecks occurring during invasions can be expected to have important consequences on variation present in invasive populations, at both genetic and phenotypic levels. Changes in genetic variation have been the focus of intense study since the formal beginning of the field of invasion genetics (Baker and Stebbins, 1965; reviewed in Dlugosch et al., 2015a). During this time, and most notably over the past two decades, molecular marker surveys have shown that sizeable reductions in genetic polymorphism are possible (Hollingsworth and Bailey, 2000). This extreme does not appear to be the norm, however, as most invasive species sustain only moderate reductions in population genetic diversity (10–20%; Dlugosch and Parker, 2008). Here, while drawing from previous empirical and modelling studies on the genetic consequences of bottlenecks, we focus on changes in phenotype. We review evidence that introduction bottlenecks are the drivers of trait divergence between native and introduced ranges and highlight, where possible, the impact on traits that may contribute to invasion success.

The extent to which introduction bottlenecks may drive changes in mean phenotypes between native and introduced ranges depends on the interaction of multiple factors, most notably the characteristics of the bottleneck and the genetic architecture of the traits in question (Dlugosch and Parker, 2008). Theoretical work has established that important reductions in heterozygosity and number of alleles will occur when population sizes are considerably reduced and also followed by slow subsequent population growth (Wright, 1931). Such conditions are expected to lead to increased inbreeding depression. If bottlenecks are intermediate in size, however, they may occasionally be beneficial. Specifically, under such conditions, the purging of deleterious mutations may occur (Facon et al., 2011; see Section 4.1 for a detailed description of dynamics in mutation load). From a trait

perspective, it has been proposed that such bottleneck-mediated reductions of inbreeding depression may facilitate transitions from outcrossing to selfing (Lande and Schemske, 1985). Modelling results indicate, however, that purging effects are often temporary, and that transitions to selfing are likely to occur only under a restricted set of conditions (Kirkpatrick and Jarne, 2000).

Genetic architecture is another important consideration (Dlugosch et al., 2015a). For traits controlled by one or a few loci, changes are expected to follow more closely predictions from population genetic theory outlined earlier. Specifically, introduction bottlenecks may drive large shifts in diversity at key loci, resulting in important changes in the mean phenotype between native and introduced ranges. Kliber and Eckert (2005) provided an example of one such important trait change mediated by an introduction bottleneck. In native (European) populations of flowering rush (*Butomus umbellatus*), triploids, which are sterile, were found to occur at higher frequencies than diploids, which are fertile (84% triploids vs. 16% diploids). In invasive (North American) populations, however, these ratios were reversed (29% sterile triploids vs. 71% fertile diploids). This pattern could have been generated if selection in the introduced range favoured sexual genotypes, which have a dispersal advantage over sterile genotypes that spread only via vegetative reproduction (Kliber and Eckert, 2005). Population genetic data excluded this possibility, however, and provided evidence that spread of *B. umbellatus* across North America occurred almost exclusively by clonal propagation (Kliber and Eckert, 2005). This result therefore implicates a founder effect as the major driver of divergence in cytotype frequency between ranges.

By contrast, for highly quantitative traits, introduction bottlenecks are expected to lead to more limited change. This is because, contrary to molecular marker polymorphism, quantitative genetic variation should be minimally impacted by the loss of rare alleles occurring during bottlenecks (Lewontin, 1965). Multiple lines of evidence support this prediction. For one, in a study of common garden data from 22 invasive plant species, population differentiation in quantitative traits was inferred to be only marginally higher in the native range than in the introduced range (3.5%; Colautti and Lau, 2015). In addition, frequent evidence for adaptive trait divergence occurring during invasions is consistent with sufficient additive genetic variation being maintained following introduction bottlenecks (Bock et al., 2015). Lastly, a recent meta-analysis re-affirmed the disconnect between molecular marker polymorphism and invasive status (Uller and Leimu, 2011). This is expected if demographic bottlenecks do not significantly impact quantitative genetic variation that is needed for adaptive evolution in traits conferring invasion success.

Aside from the question of whether introduction bottlenecks induce important trait divergence between native and introduced ranges, it may be important to consider the impact of such non-adaptive changes on

subsequent adaptive differentiation. In the flowering rush example highlighted above, evidence indicates that the founder effect set the stage for the evolution of increased clonality in invasive diploids (Klüber and Eckert, 2005). Experimental evolution studies also indicate that the phenotypic signature of strong demographic bottlenecks can be propagated during adaptive divergence over multiple generations (Kolbe et al., 2012). It could therefore be informative to partition observed trait differentiation into adaptive and non-adaptive components. Schrieber et al. (2017) performed such an analysis in comparisons of trait differentiation among native and introduced populations of *Silene latifolia*. To quantify the amount of variance attributable to non-adaptive evolution, the authors compared models with and without corrections for population co-ancestry. Results showed that phenotypic divergence among ranges was driven primarily by adaptive evolution, with a limited influence from non-adaptive processes (Schrieber et al., 2017).

3.2 Adaptive Divergence in Response to the Biotic Environment

During invasion, drastic alterations in the biotic environment are expected, including changes in the composition and abundance of herbivores, pathogens, competitors, and mutualists (Keane and Crawley, 2002; Colautti et al., 2004). Indeed, one of the most well-known and influential hypotheses relating to trait evolution in invasive species is the evolution of increased competitive ability (EICA). Invoking optimal defence theory, Blossey and Notzold (1995) hypothesised that an escape from natural enemies in the introduced range will shift allocation of resources away from defence to growth or reproduction, facilitating the evolution of a more “invasive” phenotype. They predicted that: (i) introduced populations will produce more biomass than native populations; and (ii) specialist herbivores will show improved performance on introduced populations relative to native populations.

The EICA hypothesis has spurred a large number of common garden comparisons of native and introduced populations (Blumenthal and Hufbauer, 2007; Joshi et al., 2014) along with several reviews and meta-analyses (Bossdorf et al., 2005; Colautti et al., 2009; Orians and Ward, 2010; Felker-quinn et al., 2013). These data have provided ample evidence for evolutionary shifts in traits related to reproduction, growth, defence, and competitive ability in many invasive species, but not necessarily in the direction predicted by EICA (Felker-quinn et al., 2013; Colautti and Lau, 2015). One exception appears to be size, which generally increases during invasion (Blumenthal and Hufbauer, 2007; Felker-quinn et al., 2013), but this may be mediated in some cases by differences in the climate of the sampled populations within each range (Colautti et al., 2009; Colautti and Lau, 2015). This finding supports the observation by Crawley (1987) that many invasive populations appear to be more

vigorous than their native counterparts, which motivated the initial positing of EICA. However, the hypothesis that herbivore release results in shifts in resource allocation from defence to other functions that could enhance invasion is not well supported.

A critical component of EICA is an assumption that performance in the native range is hampered by investment in herbivore defence. Yet, few studies considering EICA estimate genetic correlations between defence and performance traits and those that do typically fail to detect the predicted trade-off (Franks et al., 2008; Schrieber et al., 2017). For example, in *Silene latifolia*, although there was evidence for the evolution of lower herbivore resistance and higher performance in invasive populations that likely reflected adaptive divergence, significant negative genetic correlations between those traits were not identified in either range (Schrieber et al., 2017). This suggests each trait was evolving independently of one another in the introduced range, contrary to predictions.

EICA assumes that there are changes in resource allocation between only two competing functions. However, trade-offs may not be apparent if reduced investment to other processes, such as abiotic stress tolerance, facilitates increased performance while maintaining high levels of defence (Mole, 1994; Züst and Agrawal, 2017). Differences in resource acquisition ability among genotypes can also impact the manifestation of trade-offs (van Noordwijk and de Jong, 1986) and cause divergence in the direction of genetic correlations between populations that have evolved differences in their allocation strategy (Uesugi et al., 2017). Furthermore, resource limitation often can reveal hidden trade-offs between defence and performance (Züst et al., 2015; Züst and Agrawal, 2017). This implies that shifts in resource abundance during invasion might interact with changes in community composition to impact the evolutionary trajectory of performance and defence traits. Finally, a greater mechanistic understanding of plant defence is revealing that trade-offs typically result from antagonistic crosstalk among hormone pathways rather than the direct result of allocation costs (Karasov et al., 2017). For example, the defence hormone jasmonic acid, which is often triggered by herbivory, is known to have antagonistic effects through a complex web of interactions on growth hormones, such as auxin, brassinosteroids, and gibberellins (for a detailed review see Huot et al., 2014; Züst and Agrawal, 2017; Karasov et al., 2017).

Direct costs of defence, such as toxicity to the plant of chemical defence traits or allocation costs, are not the only factors that may govern the evolution of growth, competition, and defence-related traits during invasion. Ecological costs require interactions with another species to be expressed (Strauss et al., 2002). For instance, the production of chemical defences could attract specialist herbivores or deter important mutualists, limiting fitness (Züst and Agrawal, 2017). Indeed, it is likely that ecological costs change during invasion, highlighting the importance of measuring the fitness effects of traits in

ecologically relevant conditions. For instance, later refinements to EICA identified the need to assess competitive ability in competition trials due to the effects of traits that enhanced performance in a context-dependent way, such as allelopathic chemicals (Callaway and Ridenour, 2004; Bosssdorf et al., 2005).

Several other hypotheses concerning trait evolution in invasive populations in response to the biotic environment have been developed (Callaway and Ridenour, 2004; Beaton et al., 2011). For instance, the shifting defence hypothesis proposed that specialist targeted defences should decline while generalist targeted defences should be maintained or even increase in response to invasion (Müller-Schärer et al., 2004; Joshi and Vrieling, 2005; Doorduyn and Vrieling, 2011). In Felker-Quinn et al.'s (2013) meta-analysis, evidence for reduced defences in response to herbivores absent in the introduced range was identified. However, non-significant trends in the predicted directions were identified for both generalist and specialist herbivores. These findings suggest that evolution of defence response may be very specific to particular changes in the composition and abundance of the herbivore community.

3.3 Adaptive Divergence in Response to the Abiotic Environment

Experimental and observational studies have demonstrated that increased resource availability can enhance invasion (Davis et al., 2000; Blumenthal, 2006; Richardson and Pyšek, 2006). Moreover, species dominant in resource-rich habitats tend to exhibit traits related to invasion, such as high fecundity, fast tissue turnover, and rapid growth (Blumenthal, 2006; Leishman et al., 2007; Blumenthal et al., 2009). Grime (1977) hypothesised that traits favouring rapid growth rates should be disadvantageous in conditions of high environmental stress (He et al., 2010). Therefore, if introduced populations benefit from increased resource availability, the evolution of higher growth rates is expected and may come at the cost of abiotic stress tolerance. In keeping with this observation, several species in the Asteraceae have enhanced size and reproduction in introduced populations compared to native populations, while abiotic stressors (mainly drought) have reduced and even reversed this performance advantage in common gardens (He et al., 2010; Hodgins and Rieseberg, 2011; Turner et al., 2014; Dlugosch et al., 2015b; Hodgins et al., 2015; but see Turner et al., 2015).

But what could drive associations between invasion and resource availability, since resource abundance is not necessarily expected to increase consistently across the invaded range of the exotic species? Several studies point to biotic interactions as a means by which resource availability can be enhanced during invasion, including through escape of natural enemies (Blumenthal, 2006; Blumenthal et al., 2009), and reductions in competition (Orians and Ward, 2010). For example, loss of native grassland species in California appears to have created a vacant niche, increasing water resource

availability for invasive yellow starthistle and facilitating the evolution of larger yet less drought-tolerant populations (Dlugosch et al., 2015b). This study reveals how functional changes in community structure can drive the evolution of traits potentially contributing to invasion success, mediated through adaptation to abiotic conditions.

Although climate niche was thought to be relatively conserved between the native and introduced range (Petitpierre et al., 2012), a recent large-scale study of niche shifts during invasion found widespread evidence of differences, including evidence for climate niche expansion (analogous climates in the ranges but the climate niche has expanded in the introduced range), and pioneering (no analogous climate between native and introduced range) (Atwater et al., 2018). These climate niche shifts might reflect changes to the fundamental or realised niche but point to the widespread potential for climate-mediated selection on plant traits during invasion that could contribute to trait divergence among ranges. For example, contrary to predictions of EICA, in *Senecio pterophorus*, populations from three non-native regions were smaller and had lower reproductive output than native range plants, likely reflecting adaptation to severe summer drought stress found in these regions rather than response to changes in the biotic environment (Colomer-Ventura et al., 2015).

The EICA hypothesis has been instructional in that it has spurred studies that have improved our understanding of how and if performance, competition, and defence traits are diverging between the native and introduced ranges. These findings suggest that the adaptive landscape is dynamic, shifting in response to both biotic and abiotic changes during invasion and impacting the evolution of multivariate traits. Moreover, it has highlighted challenges that must be overcome to successfully test if adaptation to the environment experienced in the invaded range has occurred. Indeed, it is becoming clear that divergence of traits among populations within the introduced range is a common feature of plant invasions (Colautti et al., 2009; Colautti and Barrett, 2013). Therefore, experimental tests for adaptive divergence between the ranges, especially in widespread species that are occurring in spatially heterogeneous environments, which would be expected in a successful invader, require a large number of transplant gardens in the native and introduced range, extensive population sampling, as well as an understanding of the source populations for the invasion (Colautti and Lau, 2015). Such experiments are logistically challenging and can provide mixed results. For instance, a multiyear study using seven common gardens located in the native range and two introduced ranges of the tree *Triadica sebifera* found no evidence of fitness trade-offs across ranges but more frequently identified enhanced growth rates of the introduced populations in most gardens. However, the most salient finding was the large differences that emerged among common gardens and years (Siemann et al., 2016). Traits can also evolve over time within the introduced range

as a result of non-equilibrium dynamics following expansion (see Sections 4.1 and 4.2), or in response to changing selection pressures, such as when intra-specific competition (Huang and Peng, 2016) or herbivory intensifies (Gruntman et al., 2017) which might be expected in long-established populations following range expansion. Such temporal and spatial heterogeneity within the introduced range complicates comparisons of trait evolution between ranges.

3.4 Hybridisation

Hybridisation has been put forward as a stimulus for the evolution of invasiveness (Abbott, 1992; Ellstrand and Schierenbeck, 2000; Hovick and Whitney, 2014). In this section, we first discuss the genetic and phenotypic consequences of hybridisation and how they might facilitate or hinder invasiveness. We then evaluate the strength of the evidence supporting an important role for hybridisation in plant invasions. We consider interspecific hybridisation only, while recognising that similar mechanisms are operative when there is admixture involving divergent populations within a species (Rius and Darling, 2014).

Genetic and phenotypic consequences of hybridisation include the following:

- Increased genetic variation. Botanists have long recognised that hybridisation can increase the genetic diversity of hybridising populations. For example, Anderson (1949) argued that 'If introgression proves to be a primary factor in evolution it will be because it so greatly enriches variation in the participating species ...' For invading populations, such variation may be exploited by selection to increase local adaptation, potentially rescuing maladapted and genetically depauperate founding populations (i.e. evolutionary rescue). New mutations will arise more slowly and are less likely to have beneficial effects than alleles provided by hybridisation, which have already been tested by selection (Pfennig et al., 2016).
- Creation of novel, transgressive phenotypes. Hybrids often exhibit non-additive trait expression, including extreme (transgressive), novel, or missing traits (Rieseberg and Ellstrand, 1993). Transgressive trait values typically arise from complementary gene action, in which parental alleles with effects in the same direction are over-represented in individual hybrid genotypes (Rieseberg et al., 1999; Stelkens and Seehausen, 2009). Novelty or loss of traits has many possible causes. For example, the gain and loss of chemical compounds in hybrids has been attributed to the inhibition of biosynthetic pathways, pathway elaboration via new combinations of chemical skeletons and side-chains, and altered gene regulation (Orians, 2000). Non-additive trait expression is frequently linked to the colonisation of new environments (Stelkens et al., 2014),

and shifts in chemical constituents may reduce the efficacy of biological control strategies (Gaskin, 2017).

- Heterosis. Early generation hybrids often exhibit increased vigour or heterosis. While the masking of deleterious recessive mutations in hybrids (dominance) is thought to be the main cause of heterosis (Yang et al., 2017), overdominance (in which heterozygotes are superior to either homozygous class at a single locus) and epistasis contribute as well. Heterosis can be fixed in asexual and polyploid hybrids, likely contributing to their over-representation in invasive taxa (Schierenbeck and Ellstrand, 2009; Pandit et al., 2011).
- Genetic rescue. Due to founding events and extreme drift during invasive spread, invaders may suffer from inbreeding depression and genetic load (Peischl et al., 2013). Hybridisation offers a means of rescuing such populations by providing superior alleles that can complement or replace deleterious variants (Ellstrand and Schierenbeck, 2000; Conte et al., 2017).
- Demographic rescue. Invading populations may also suffer reduced fitness for purely demographic reasons, such as pollination limitation. A recent theoretical study indicates that hybridisation can rescue populations experiencing Allee effects (i.e. reduced fitness due to low density), without invoking other favourable consequences of hybridisation (Mesgarana et al., 2016). The same study suggests that invasions of European searockets (*Cakile maritima*) likely involved such a mechanism.
- Outbreeding depression. Hybridisation can have negative consequences as well. Hybrid populations often suffer from outbreeding depression due to chromosomal re-arrangements, genic incompatibilities, and/or a disruption of adaptation to the local environment (Baack et al., 2015). If outbreeding depression is strong, population growth rates of hybrid invaders might drop below replacement rates, leading to extinction.
- Genetic swamping. If founding populations are small relative to a sympatric or parapatric congener, and barriers to mating are weak, new invaders may also lose their genetic and phenotypic identity, and possibly key invasiveness traits, via genetic swamping (Todesco et al., 2016).

So do the potentially positive consequences of hybridisation outweigh possible negatives in the context of plant invasions? Numerous hybrid invaders have now been documented (reviewed in Ellstrand and Schierenbeck, 2000; Schierenbeck and Ellstrand, 2009; Gaskin, 2017), and several experimental studies have established hybridisation as a causative factor in plant invasions (Vila and D'Antonio, 1998; Campbell et al., 2006; Whitney et al., 2006; Hooftman et al., 2007; Parepa et al., 2014). A recent meta-analysis of 15 systems in which hybridisation has been putatively associated with invasiveness indicates that wild hybrids are significantly larger and more fecund than their parental species (Hovick and Whitney, 2014). Also, fecundity increases with

hybrid generation, implying that natural selection is acting to increase hybrid performance.

On the other hand, an earlier comparative analysis indicated that hybridisation-prone plant families do not produce more invasive species (Whitney et al., 2009). Also, outcomes of hybridisation are context dependent and vary depending on the genetic distance of the cross, hybrid class, and environmental conditions (Stelkens et al., 2014; Hovick and Whitney, 2014). Thus, while hybridisation may facilitate some invasions, we cannot rule out the possibility that it hampers an equal or greater number of other invasions, even in the same system. We see two main ways to address this issue. First, genome-based methods for detecting hybridisation (Payseur and Rieseberg, 2016) offer a means for increasing the power and resolution of comparative studies of hybridisation and invasion. Such methods could also be used to distinguish between auto- and allopolyploids, making it possible to disentangle the roles of hybridisation and genome duplication in invasiveness (Pandit et al., 2011). Second, as emphasised by Hovick and Whitney (2014), experimental and theoretical studies that explore the effects of genetic distance, hybrid genotype, and environment on the outcomes of hybridisation would increase our ability to understand and predict its role in invasion success.

3.5 Evolution of Phenotypic Plasticity During Biological Invasions

Phenotypic plasticity, commonly defined as the ability of the same genotype to produce alternative phenotypes when exposed to different environments, has long been suspected to contribute to biological invasions (Baker, 1965). This is because plasticity should allow introduced genotypes to adjust to novel environmental conditions within a generation, without the need for genetic variation to be present or for adaptive evolution to occur. While this assumption is intuitive, support for a causative role of phenotypic plasticity in biological invasions has so far been mixed (Davidson et al., 2011; Palacio-Lopez and Gianoli, 2011). The evolution of phenotypic plasticity during the invasion process has been proposed as a possible explanation for these inconsistent findings (Lande, 2015).

That important changes in plasticity can evolve over the course of only a few generations has been known for more than half a century. For example, in 1953, Conrad Waddington showed that under artificial selection in the laboratory, an environmentally induced trait in *Drosophila melanogaster* can lose plasticity and become constitutively expressed (Waddington, 1953). Rapid evolutionary gains in plasticity have also been documented, such as those that accompanied the divergence of *Phlox drummondii* cultivars from wild populations (Schlichting and Levin, 1988). In natural settings, an early example of microevolutionary shifts in plasticity was provided by Cook and Johnson (1968). Using a common garden experiment in which

Ranunculus flammula genotypes were grown under terrestrial or under aquatic conditions, the authors demonstrated among-population differences in responses of leaf morphology to environment. In this case, results strongly indicated that evolved differences are also adaptive. This is because levels of phenotypic plasticity in each population were correlated with field measurements of environmental heterogeneity. As well, survival experiments linked estimates of plasticity with differences in mortality under controlled and under field conditions (Cook and Johnson, 1968).

Examples such as those highlighted above raised the question of whether rapid evolution of plasticity is common. To answer this, Murren et al. (2014) performed a meta-analysis comparing trait means and plasticities among congeneric animal and plant species and among populations within species. Results confirmed that evolutionary changes in plasticity occur frequently (Murren et al., 2014). Moreover, the magnitude of observed shifts in plasticity was comparable to or larger than that of observed changes in trait means (Murren et al., 2014). The same analysis produced two additional results that are of relevance for trait evolution in invasive species. First, across the dataset, plasticity evolved more frequently for reproductive and for physiological traits, than for morphological traits. This is notable because traits categorised as reproductive or physiological are expected to have an important contribution to invasive spread (see Section 2). Second, larger evolutionary changes in plasticity were identified when populations or species were exposed to conditions outside their normal environmental range, a scenario that may occur frequently during biological invasions. This is consistent with Schlichting (2008), who indicated that novel environments and/or novel genomic backgrounds that result from hybridisation or polyploidisation can reveal cryptic genetic variation in reaction norms, spurring rapid evolution of plasticity.

Theoretical models have investigated the conditions under which phenotypic plasticity is likely to evolve. Among these, models that consider major shifts in environment can be considered as broadly applicable to the evolution of plasticity during biological invasions (reviewed in Lande, 2015). Lande (2009), for example, modelled a population in which genotypes differ in trait means and degree of plasticity, and tracked its dynamics following an important and sudden change in environment. In this case, plasticity was inferred to be non-labile, such that adult phenotypes are determined by the environment that the juveniles experience during a critical stage in development. Adaptation to the new range occurred in two phases. During the first phase, which can be referred to as genetic accommodation (Crispo, 2007), there was a rapid evolutionary increase in adaptive plasticity, which allowed genotypes to quickly approach the phenotypic optimum in the new environment. Important reasons for this transition were that additive genetic variance for plasticity is large and that differences between the ancestral and derived environments are substantial (Lande, 2009). The second phase

involved the gradual loss of phenotypic plasticity to a level characteristic of the ancestral range, through genetic assimilation. At the completion of this phase, phenotypic values more similar to those selected for in the new locale could be produced across a broader range of environments. Important assumptions for genetic assimilation to occur are that environmental predictability is similar between ranges, and that there are costs to maintaining a highly plastic response (Lande, 2009). More recent work (Lande, 2014) has expanded on these results to also consider labile plasticity (i.e. the adult phenotype changes with environment). Results indicated a similar two-stage dynamic, although with different contributions of parameters like environment predictability or plasticity costs (Lande, 2014, 2015).

With the caveat that it is often difficult to unambiguously designate plastic responses as adaptive (Schlichting, 1986), results from common garden comparisons of native and introduced populations are broadly aligned with these theoretical predictions. Among the two phases identified by models, genetic accommodation appears to be more common, and has been reported for morphological (Kaufman and Smouse, 2001; Leger and Rice, 2003; Chun, 2011), physiological (Kaufman and Smouse, 2001; Cano et al., 2008), or reproductive traits (Leger and Rice, 2003). Support for the occurrence of genetic assimilation during biological invasions has, by comparison, been more limited (Godoy et al., 2011). One explanation for this pattern is that the end-result of genetic assimilation cannot be distinguished from evolution of trait means without changes in plasticity (Lande, 2015). Alternatively, genetic assimilation may indeed occur less frequently, potentially because plasticity costs are negligible (Murren et al., 2015; but see van Kleunen and Fischer, 2005). Further supporting this possibility is the fact that most invasive populations for which genetic assimilation has not occurred, and for which highly plastic responses appear to be maintained, are found in high-resource environments where costs are likely to be negligible (Kaufman and Smouse, 2001; Leger and Rice, 2003; Cano et al., 2008; Chun, 2011).

4 Trait Evolution Within the Introduced Range

Following introduction, a key component to invasion is range expansion. The evolution of populations initially establishing at the leading edge of a range expansion can be divided into three main stages: (i) dispersal and colonisation, (ii) initial establishment following colonisation, and (iii) longer-term evolution (Pannell, 2015). All three stages will shape trait evolution during invasion and could impact differentiation of native and introduced populations as well as divergence among introduced populations. We consider these stages below in the context of trait differentiation within the introduced range in plant invaders, with a particular focus on traits that may impact

spread, abundance, and competitive ability. Our discussion first begins with a consideration of how neutral processes during range expansion might impact evolution of these traits.

4.1 Impact of Range Expansion on Spatial Genetic Patterns and Fitness

Spatial patterns in allele frequencies or quantitative traits are often interpreted as evidence for selection; however, such patterns can also be created through neutral processes. Serial founder effects occurring during rapid range expansion can result in increasing allele frequencies at a subset of loci – a process called ‘allele surfing’ (Excoffier et al., 2009; Peischl and Excoffier, 2015; Peischl et al., 2016). Theoretical studies have demonstrated that the spatial distribution of neutral (Klopfstein et al., 2006), deleterious, and beneficial alleles (Travis et al., 2007; Hallatscheck and Nelson, 2009) can be impacted by these serial founder events both during and after expansion. Deleterious alleles can rise in frequency during range expansion (Travis et al., 2007) leading to increasing genetic load at the range edge (i.e. expansion load; Peischl et al., 2013). These deleterious mutations can spread and fix locally even if they reduce competitive ability (K) and/or moderately reduce reproductive rates (r) (Travis et al., 2007). Furthermore, expansion load can evolve due to the effects of new mutations occurring at or near the range edge, maladaptive alleles introduced via hybridisation, and from standing variation (Peischl and Excoffier, 2015). Expansion load has potentially important consequences for invasion as it can slow the rate of spread and even limit a species’ range (Peischl et al., 2015).

Although expansion load should dissipate over time, it can persist for thousands of generations (Peischl et al., 2013). Using genomic data, evidence supporting greater mutation load in populations colonising previously glaciated regions in Europe has been identified in the annual plant *Mercurialis annua* (González-Martínez et al., 2017). However, most work on the genomic signature of expansion load has been conducted in humans (Lohmueller et al., 2008; Peischl et al., 2013; Simons et al., 2014; Henn et al., 2016) where patterns consistent with increasing recessive mutation load with distance from Africa have been identified (Peischl et al., 2016; Henn et al., 2016). Experimental evolution studies in bacteria have also demonstrated patterns of genetic polymorphism and fitness consistent with expansion load (Bosshard et al., 2016). However, as of this writing, the genomic signature of expansion load has not been identified in plant invaders (Hodgins et al., 2015), although they offer opportunities to explore the impact of allele surfing on fitness and demography.

During invasion, there are several factors that might limit the evolution of expansion load, such as long-distance dispersal, negative epistatic interactions of deleterious alleles facilitating purging or admixture (Peischl

et al., 2013, 2016; Marchini et al., 2016). Furthermore, range expansions can be slowed by factors such as Allee effects and local maladaptation during expansion across an environmental gradient (Gilbert et al., 2017). Slow expansions allow selection to more effectively eliminate deleterious alleles, may permit migrants from the core harbouring non-deleterious variants to 'catch-up' to edge populations, and provide greater opportunity for back mutations, thereby mitigating expansion load (Gilbert et al., 2017). This suggests that some plant invasions, such as those involving species exhibiting strong Allee effects, local adaptation, admixture, or long-distance dispersal, might escape substantial expansion load. Furthermore, the fitness effects and demographic consequences of expansion load might be challenging to characterise in invasions if local adaptation has evolved following range expansion, which could confound non-conditionally deleterious alleles with conditionally beneficial ones (Conte et al., 2017).

Serial founder events during range expansion could have important impacts on adaptive evolution, as well as its underlying genetic architecture. Surfing of deleterious alleles can lead to an increased frequency of adaptive peak shifts during range expansion if the rugged fitness landscape is caused by sign epistasis (i.e. when a mutation has a beneficial fitness effect on one genetic background but a deleterious effect on another; Burton and Travis, 2008). Genetic drift can even increase the fixation rate of weakly beneficial mutations at the advancing front and could facilitate adaptation towards an invasive phenotype during expansion (Lehe et al., 2012). Invasive species therefore offer opportunities to explore how range expansion impacts the genetic architecture of adaptation, the rate of adaptation and, in turn, the spread the invader.

4.2 Dispersal and Colonisation

Propagule dispersal to appropriate habitats at the leading edge of an invasion is necessary for range expansion and can act as the first selective filter in this process. During expansion, individuals with high dispersal capacity should be the first to arrive at the range edge and thereby benefit from low levels of competition. If dispersal is heritable, alleles favouring high dispersal will be more frequent at the expanding wave front. Subsequent mating among high dispersers accumulating at the range edge will lead to the further production of high-dispersing genotypes that should drive accelerating range expansion over time and a gradient in dispersal capacity over space (Phillips et al., 2006, 2010; Travis et al., 2009). This process, termed spatial sorting (Shine et al., 2011), has extensive theoretical and empirical support (Travis and Dytham, 2002; Phillips et al., 2006; Travis et al., 2009; Burton et al., 2010; Ochocki and Miller, 2017). There are several well-known examples of dispersal gradients evolving during range expansion in animals (Simmons and Thomas, 2004; Phillips et al., 2006; Lombaert et al., 2014), including the cane toad invasion in

Australia, where over the past 70 years longer legs and jumping ability have increased at the leading edge of the range, causing a fivefold increase in the annual rate of expansion (Phillips et al., 2008, 2010). Therefore, the theoretical and empirical evidence is mounting that dispersal evolution during range expansion can substantially enhance the spread rate of the invader.

The process of spatial sorting was first recognised in a study examining geographic variation in seed morphology of lodgepole pine that was presumed to have evolved during post-glacial expansion (Cwynar and MacDonald, 1987). However, evidence for greater dispersal capacity at the range edge during recent plant invasions is relatively rare (Hargreaves and Eckert, 2014). The evolution of seed characteristics that favour dispersal have been identified at the range edge in some wind-dispersed introduced species such as *Gladiolus gueinzii* (Tabassum and Leishman, 2018) and *Senecio inaequidens* (Monty and Mahy, 2010; but see Lachmuth et al., 2011), but expected gradients for seed dispersal traits have not evolved in other invasive plants, such as *Senecio madagascariensis* (Bartle et al., 2013) or *Mikania micrantha* (Huang et al., 2015). From these few examples, it is difficult to determine if dispersal evolution at the range edge is a common feature of range expansion during invasion in plants.

Based on classic ecological theory, low population density at the range edge is expected to lead to r-selection, where a lack of overcrowding in a population selects for traits associated with population growth, such as increased reproduction effort (MacArthur and Wilson, 1967). As a result, both dispersal and reproductive investment are expected to evolve to be higher at the range edge (Burton et al., 2010). In a recent experimental evolution study in flour beetles, dispersal increased at the range edge as predicted during expansion. However, unexpectedly, reproductive rates declined perhaps due to the impact of expansion load (Weiss-Lehman et al., 2017). Models including trade-offs among dispersal, competition, and reproduction reveal that dispersal gradients can decay in populations relatively rapidly as high-density selects for investment in competition (Perkins et al., 2016). Similarly, interspecific competition can drive investment in competition at the leading edge of the expansion at the expense of investment in dispersal (Burton et al., 2010), and intraspecific competition generated through patchy landscapes can limit the evolution of low-density reproduction (Williams et al., 2016b). In a recent experimental evolution study in *Arabidopsis thaliana*, the evolution of competitive and dispersal ability during expansion resulted in a 200% increase in spread compared to non-evolving populations in a patchy environment (Williams et al., 2016a). By contrast, the impact of evolution in a continuous environment on spread rate was less apparent. Together, these empirical and theoretical studies reveal that trade-offs among traits, ecological interactions, and the spatial structure of suitable habitat can have a large impact on the evolution of traits that influence spread rate.

Several other factors could impact the evolution of dispersal gradients and spread rates. Allee effects in low-density populations found at the range edge or adaptation along an environmental gradient during invasion can slow range expansion and prevent dispersal gradients from evolving (Travis and Dytham, 2002; Phillips, 2012). Dispersal evolution is also contingent on other selective factors, such as temporal changes in habitat quality (Dytham, 2009; Pannell, 2015), and spatial variation in these factors could impact the evolution of dispersal gradients. Complex invasions with introductions in multiple areas of the novel range, hybridisation, or repeated ‘accidental’ long-distance dispersal events (e.g. human mediated) appear to be relatively common in plants (van Boheemen et al., 2017) and could also prevent dispersal gradients from establishing. Furthermore, stochasticity caused by serial founder events can impact the evolution of dispersal and fitness, making predictions regarding spread rate challenging (Phillips, 2015).

5 Establishment

Not only must propagules arrive at the range edge, but they must also grow and reproduce to establish a new population under low-density conditions. Therefore, a second selective filter is imposed during the establishment phase of range expansion. Baker (1955) proposed that self-compatible species will be more likely to colonise new locations due to assured reproduction when mates and/or pollinators are limited. Self-compatibility will be particularly important in annual species that reproduce sexually, and therefore have limited time to find suitable mating partners. This hypothesis, termed Baker’s law, has received substantial support through interspecific comparisons of introduced and native species (Rambuda and Johnson, 2004; van Kleunen and Johnson, 2007) and other comparisons of non-colonising and colonising taxa (Grossenbacher et al., 2017). Self-compatibility during invasion should facilitate more rapid range expansion, as suggested by Baker’s Law, as well as the evolution of dispersal gradients and expansion load by reducing Allee effects at the range edge.

Intraspecific comparisons between the native and introduced ranges have yielded relatively limited support for a breakdown of self-incompatibility during invasion (e.g. Li et al., 2012; but see Petanidou et al., 2012). Evidence for the evolution self-compatibility at the range margins during recent plant invasions is also largely absent from the literature (Barrett, 2015). For example, *Lythrum salicaria* had no pattern of increased self-compatibility towards the northern range limit in the North American introduced range (Colautti et al., 2010). It is possible that in some invasive species high levels of pollen and/or seed dispersal among patches eliminates substantial Allee effects (Pannell, 2015). Furthermore, the evolution of self-compatibility will

depend on factors such as the extent of inbreeding depression. Inbreeding depression itself can evolve, and is expected to decline in small range edge populations, due to purging and local fixation of recessive deleterious alleles, which can favour the spread of selfing variants (Pujol et al., 2009; Pannell, 2015). However, inbreeding depression can be stronger in stressful environments (Fox and Reed, 2011), and stress levels may differ both within and between the ranges (Schrieber and Lachmuth, 2016). Therefore, simple expectations concerning the evolution of self-compatibility during plant invasion may ignore important complexities that could limit or favour its evolution.

5.1 Local Adaptation

The capacity to rapidly adapt to local environmental conditions is a potential mechanism that may predispose species to invasive spread. In a recent meta-analysis of field and growth chambers experiments in invasive and native species, the signature of local adaptation in invasive species was at least as strong as in native species (Oduor et al., 2016). This is noteworthy, especially given the limited timespan of most introductions and the potential for genetic bottlenecks during invasion. Interestingly, there was no effect of reproductive system, life cycle, mating system, or time since introduction on the signature of adaptive differentiation, suggesting that adaptive evolution happens rapidly, frequently, and across an array of species types.

Invaders often expand across large climatic gradients, which can shift significantly from the climate niche experienced in the native range (Atwater et al., 2018). Such range expansion provides opportunities for divergence of quantitative traits within the introduced range that may be driven by climate-mediated selection (Maron et al., 2004; Colautti et al., 2009; Chown et al., 2015; Moran et al., 2017). In introduced populations of *Lythrum salicaria*, earlier flowering has evolved in the north where season length is shorter compared to southern locations (Colautti and Barrett, 2013). However, early flowering appears to come at the cost of reduced size and fecundity due to genetic correlations between plant size and flowering time. Therefore, delayed reproductive maturity is favoured in southern locations with longer growing seasons (Colautti and Barrett, 2010, 2013). Reciprocal transplant experiments using high-, mid-, and low-latitude locations accompanied by estimates of selection in the field have provided strong evidence for adaptive divergence of flowering time and size along the latitudinal gradient (Colautti and Barrett, 2013). Moreover, the fitness effect of adaptation along this cline is greater than that of enemy release or EICA, suggesting an important role of climate adaptation in the abundance and spread of this invader. However, few studies have conducted reciprocal transplant experiments within the introduced range to so clearly demonstrate rapid and recent adaptation to climatic gradients.

Several studies now show genetic divergence of quantitative traits in introduced populations that correlate with geographic or climatic variables, implicating selection in response to abiotic or biotic gradients (Keller et al., 2009; Hodgins and Rieseberg, 2011; Samis et al., 2012; Gallien et al., 2016). However, as discussed above, the expansion process itself can create clines in dispersal and reproductive rates through spatial sorting (Shine et al., 2011), and serial founder events can generate non-adaptive geographical clines in allele frequencies and multilocus traits (Klopfstein et al., 2006; Travis et al., 2007; Peischl et al., 2013; Colautti and Lau, 2015). Multiple introductions could also create a patchwork of trait variation across the invaded landscape that might be mistakenly taken as evidence for adaptive trait divergence, but could simply reflect introduction history. Climate matching (Maron et al., 2004) occurs when introductions are sourced from similar climatic regions in the native range. Under this scenario, pre-adaptation could be instrumental in the evolution of adaptive patterns of trait divergence in the introduced range rather than *in situ* rapid local adaptation.

In the absence of pre-adaptation and climate matching, repeated parallel patterns of quantitative traits with climate of origin are unlikely to frequently evolve through neutral processes and can provide support for local adaptation (Stock et al., 2014; Yeaman et al., 2016). A complementary approach to provide evidence of adaptive divergence along a climatic gradient is to compare patterns in quantitative traits or their associated loci to background patterns of differentiation at putatively neutral markers (Lachmuth et al., 2011; Agrawal et al., 2015). However, recent range expansion, multiple introductions, and admixture are demographic processes that can create spatial patterns in allele frequencies. Using this method to infer selection in populations experiencing these demographic changes could potentially cause either high false positive or false negative rates depending on the demographic scenario. This approach is somewhat analogous to Qst-Fst tests of selection for quantitative traits, which can also be prone to incorrect inferences in the invasion context (Colautti and Lau, 2015). Therefore, further investigations of these demographic changes on tests of selection for polygenic traits are warranted.

6 Trait Evolution in Crop-derived Invasive Species

Plant cultivation has long been recognised as an important vector of biological invasions (Reichard and White, 2001). Well-known examples of crop-derived invasives that have become problematic in agricultural settings and/or in natural communities include California wild radish, weedy rice, or weedy rye (Ellstrand et al., 2010). Such invasives may originate directly from a crop, or they may represent a product of hybridisation among

crops, or between crops and wild taxa. Here, we summarise examples of trait evolution in invasive species that have a crop ancestry. We contrast patterns of trait divergence observed in these crop-derived invasive taxa with patterns discussed above for invasive taxa that derive exclusively from wild progenitors, following long-distance human-mediated colonisation.

As compared to invasive species that are strictly wild derived, crop-derived invasives often originate in sympatry with their cultivated and wild progenitors. Under these conditions, gene flow from crop or wild parental populations to the emerging invader may represent an important barrier to the establishment of self-sustaining invasive populations (Ellstrand et al., 2010). It is perhaps not surprising, therefore, that shifts to earlier or to delayed flowering has been reported in a number of invasive crop derivatives (Burger et al., 2007; Ellstrand et al., 2010). If barriers to gene flow do not evolve, and if the fitness of the invasive taxon is comparable to or higher than that of its progenitor(s), the extinction of naturally occurring parental taxa via genetic swamping may occur (Todesco et al., 2016). A well-known example is that of California wild radish, an invasive hybrid that contributed to the local extinction of naturalised populations of its progenitors, *Raphanus sativus* and *Raphanus raphanistrum* in California (Hegde et al., 2006).

Further trait divergence may involve the rapid evolutionary loss of crop-like traits, commonly referred to as de-domestication. While exceptions have been found (see the following text), de-domestication has emerged as one of the most consistent findings of trait comparisons between crops and invasive derivatives (Ellstrand et al., 2010). The traits undergoing de-domestication are often in the same category as those hypothesised to contribute to the success of wild-derived invasive species (see Section 2). One example is shattering. While crops are typically selected to be non-shattering (i.e. the seeds are not dispersed at maturity and instead remain on the plant until harvest), crop-derived invasives frequently show a reversal to high shattering rates characteristic of wild taxa (Londo and Schaal, 2007; Thurber et al., 2010). This condition is expected to facilitate dispersal. Other traits also thought to facilitate spread or persistence that have undergone reversal to a wild-type form include increased number of fruits and seeds per plant and seed dormancy (Ellstrand et al., 2010).

Occasionally, however, the same traits that have been selected for by breeders prove to be beneficial for invasive species as well. In this case, crop-like traits will continue to be selected for in invasive genotypes. For invasive species spreading in agroecosystems, examples include crop mimicry, herbicide tolerance, and high selfing rates (Snow and Campbell, 2005; Delouche et al., 2007). In natural ecosystems as well, some crop-like traits can be advantageous. One well-known example is breeding for bioenergy crops, which often selects for traits that can drive invasions, like increased biomass or wide environmental tolerance (Barney and DiTomaso, 2008). Campbell et al. (2009) investigated the possibility that crop-like traits

continued to be selected for in natural settings using experimental evolution in radish (*Raphanus* spp.). Crop × wild hybrid populations and wild populations were grown under semi-natural conditions, and trait divergence was tracked for three generations. Results showed that some crop traits, like the production of larger numbers of flowers and larger root diameters were consistently favoured by selection in the hybrid populations. Further, there was evidence that evolution of other potentially beneficial traits, such as earlier reproduction, was constrained by phenotypic correlations (Campbell et al., 2009).

Recent studies have taken such field experiments one step further, and complemented screens of phenotypic divergence with those of genomic divergence. Corbi et al. (2017) for example, used a crop × wild sunflower (*Helianthus annuus*) population to investigate the trajectory of crop-like traits and alleles in a hybrid. Sunflower contains weedy genotypes that are problematic in agricultural ecosystems. Previous studies have indicated that such weedy forms may have originated repeatedly from nearby wild genotypes (Kane and Rieseberg, 2008). The population used by Corbi et al. (2017) was allowed to evolve under natural conditions at two locations, over two generations (Figure 1). Results showed either no trait differentiation between generations or a significant change towards the wild parent. At both locations, for example, plants transitioned to delayed flowering, smaller seeds, and increased plant height. In line with these observations, selection overwhelmingly favoured wild-like alleles. In a few cases (i.e. for an estimated 8% of markers), there was evidence of selection driving increases in the frequency of crop-derived alleles. This supports previous findings that domesticated gene pools can contain alleles that confer increased fitness in the wild. The origin of such alleles in the sunflower system is currently unknown, and may include crosses with congeners during breeding, or beneficial mutations arising during the domestication process (Corbi et al., 2017).

7 Conclusions and Future Directions

Our overview of theoretical and empirical studies of plant invasions identifies conclusions that can be made about trait evolution and suggests fruitful directions for future research. We now know, for example, that rapid phenotypic evolution is the rule rather than the exception during invasions, that population bottlenecks have limited impacts on quantitative trait variation and on the evolution of invasiveness traits, and that phenotypic differences between populations from the native and invasive range are predominantly a consequence of adaptation rather than drift (although there are some exceptions). There has also been some success in identifying traits associated with

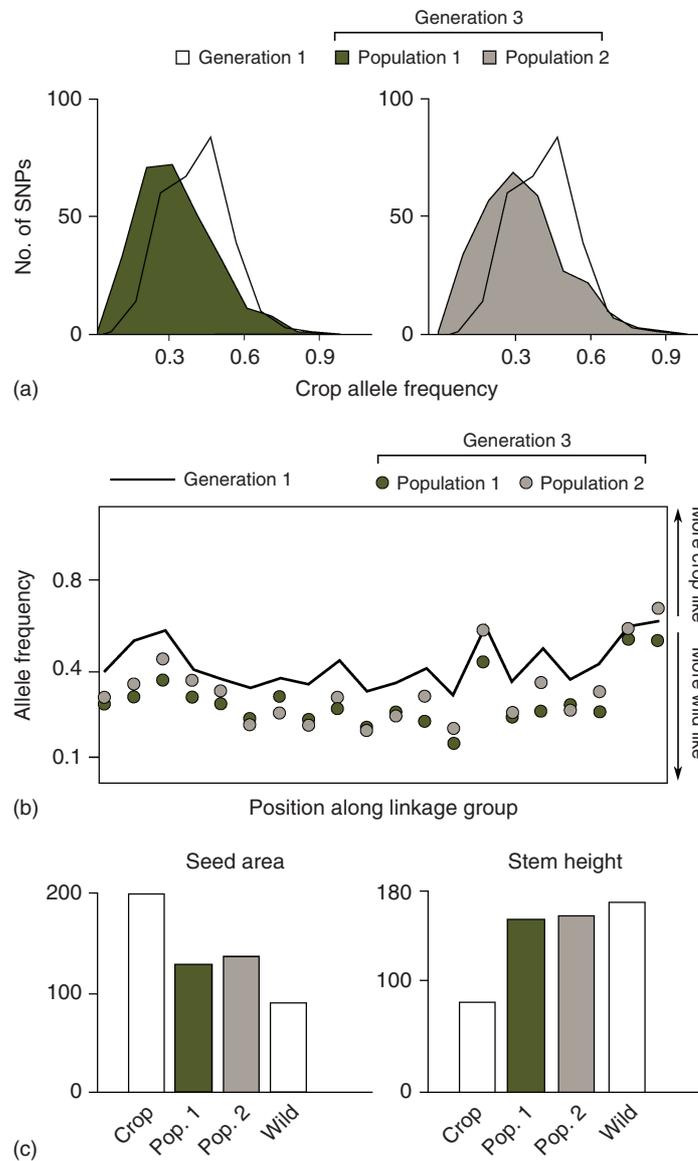


Figure 1 Evolution of experimental crop x wild sunflower populations (modified from Corbi et al., 2017). After three generations, crop allele frequencies are reduced, as both populations evolve towards the wild parent. Changes in allele frequency are presented either genome-wide (a), or along one of the linkage groups of the sunflower genome (b). Phenotypically as well, both populations evolved to be more wild-like (c). Results are given for seed area and stem height, as estimated in one of the two common gardens.

successful establishment and range expansion, although much uncertainty remains.

On the other hand, little support has been found for the influential EICA hypothesis. Rather, studies testing it indicate that the fitness landscapes experienced by invaders are surprisingly complex and dynamic. This body of work has also drawn attention to the need for multiple common gardens in both the native and introduced range to robustly demonstrate local adaptation of invasive populations.

Numerous puzzles remain. For example, we do not yet have sufficient data to determine whether range edge populations typically exhibit increased dispersal ability and/or expansion load as predicted by theory. The role of hybridisation in plant invasions represents another puzzle. While shown to facilitate some invasions, the possibility that hybridisation impedes an equivalent number cannot be ruled out. Here, a combination of new genomic and comparative methods may offer a solution. Likewise, plasticity's impact on invasions remains uncertain, with some studies reporting a causative role for phenotypic plasticity and others finding no significant contribution. Evolutionary change in plasticity during the invasion process represents a possible explanation for these contradictory reports. Thus, studies of plasticity that account for invasion stage should be a priority going forward. It is also critical to sort out whether the changes in plasticity are adaptive and for which traits plasticity is critical to invasion success.

Lastly, there have been repeated suggestions in the literature that the lag phase of invasion, where the invader is present but at low abundance, might be due in some cases to maladaptation to the local environment, while the population size increase that follows reflects subsequent adaptation (Crooks, 2005; Bock et al., 2015). It is often assumed that local adaptation will enhance reproductive rates and carrying capacity during invasion, but the impact of local adaptation on spread and abundance is not well understood empirically (Gomulkiewicz et al., 2010; Hendry, 2016). Local adaptation could reflect the outcome of competition among conspecific genotypes within a patch (i.e. soft selection; Lowe et al., 2017). Under this scenario, adaptation does not impact local population size, and populations composed of maladapted genotypes relative to hypothetical optima could still result in invasion (Hendry, 2016). Although challenging, future empirical work on the ecological impact of adaptive trait evolution in invasive species should seek to explicitly link local adaptation and key demographic parameters influencing spread rate and abundance.

Over the past half century, the study of trait evolution in invasive populations has been driven as much by an interest in understanding fundamental evolutionary processes as in predicting invasion success. We do not expect this to change. The replicated introductions provided by invasive plants offer a powerful means for studying the predictability of evolution at both the phenotypic and genomic scale, and perhaps most importantly, the

repeatability of eco-evolutionary feedbacks. Such information may not only help identify taxa and habitats that are prone to invasions but may also provide clues regarding how populations, species, and communities will respond to climate change.

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References

- Abbott, R.J. (1992). Plant invasions, interspecific hybridization and the evolution of new plant taxa. *Trends in Ecology & Evolution* **7**: 401–405.
- Agrawal, A., Hastings, A., Bradburd, G. et al. (2015). Evolution of plant growth and defense in a continental introduction. *The American Naturalist* **186**: E1–E15.
- Anderson, E. (1949). *Introgressive Hybridization*. New York: Wiley.
- Atwater, D.Z., Ervine, C., and Barney, J.N. (2018). Climatic niche shifts are common in introduced plants. *Nature Ecology & Evolution* **2**: 34–43.
- Baack, E., Melo, M.C., Rieseberg, L.H., and Ortiz-Barrientos, D. (2015). The origins of reproductive isolation in plants. *New Phytologist* **207**: 968–984.
- Baker, H. (1955). Self-compatibility and establishment after ‘long-distance’ dispersal. *Evolution* **9**: 347–349.
- Baker, H.G. (1965). Characteristics and modes of origin of weeds. In: *The Genetics of Colonizing Species* (ed. H. Baker and G. Stebbins), 147–168. New York: Academic Press.
- Baker, H.G. (1974). The evolution of weeds. *Annual Review of Ecology and Systematics* **5**: 1–23.
- Baker, H.G. and Stebbins, G.L. (ed.) (1965). *The Genetics of Colonizing Species*. New York: Academic Press.

- Barney, J.N. and DiTomaso, J.M. (2008). Nonnative species and bioenergy: are we cultivating the next invader? *Bioscience* **58**: 64–70.
- Barrett, S.C.H. (2015). Foundations of invasion genetics: the Baker and Stebbins legacy. *Molecular Ecology* **24**: 1927–1941.
- Bartle, K., Moles, A.T., and Bonser, S.P. (2013). No evidence for rapid evolution of seed dispersal ability in range edge populations of the invasive species *Senecio madagascariensis*. *Austral Ecology* **38**: 915–920.
- Beaton, L.L., van Zandt, P.A., Esselman, E.J., and Knight, T.M. (2011). Comparison of the herbivore defense and competitive ability of ancestral and modern genotypes of an invasive plant, *Lespedeza cuneata*. *Oikos* **120**: 1413–1419.
- Blossey, B. and Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology* **83**: 887–889.
- Blumenthal, D.M. (2006). Interactions between resource availability and enemy release in plant invasion. *Ecology Letters* **9**: 887–895.
- Blumenthal, D.M. and Hufbauer, R.A. (2007). Increased plant size in exotic populations: a common-garden test with 14 invasive species. *Ecology* **88**: 2758–2765.
- Blumenthal, D., Mitchell, C.E., Pysek, P., and Jarosik, V. (2009). Synergy between pathogen release and resource availability in plant invasion. *PNAS* **106**: 7899–7904.
- Bock, D.G., Caseys, C., Cousens, R.D. et al. (2015). What we still don't know about invasion genetics. *Molecular Ecology* **24**: 2277–2297.
- Boheemen, L.A., van Lombaert, E., Nurkowski, K.A. et al. (2017). Multiple introductions, admixture and bridgehead invasion characterize the introduction history of *Ambrosia artemisiifolia* in Europe and Australia. *Molecular Ecology* **26**: 5421–5434.
- Bone, E. and Farres, A. (2002). Trends and rates of microevolution in plants. *Genetica* **8**: 165–182.
- Bossdorf, O., Auge, H., Lafuma, L. et al. (2005). Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* **144**: 1–11.
- Bosshard, L., Dupanloup, I., Tenaillon, O. et al. (2016). Accumulation of deleterious mutations during bacterial range expansions. *Genetics* **207**: 669–684.
- Burger, J.C., Holt, J.S., and Ellstrand, N.C. (2007). Rapid phenotypic divergence of feral rye from domesticated cereal rye. *Weed Science* **55**: 204–271.
- Burton, O.J. and Travis, J.M.J. (2008). The frequency of fitness peak shifts is increased at expanding range margins due to mutation surfing. *Genetics* **179**: 941–950.
- Burton, O.J., Phillips, B.L., and Travis, J.M.J. (2010). Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* **13**: 1210–1220.
- Callaway, R.M. and Ridenour, W.M. (2004). Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* **2**: 436.
- Campbell, L.G., Snow, A.A., and Ridley, C.E. (2006). Weed evolution after crop gene introgression: greater survival and fecundity of hybrids in a new environment. *Ecology Letters* **9**: 1198–1209.
- Campbell, L.G., Snow, A.A., and Sweeney, P.M. (2009). When divergent life histories hybridize: insights into adaptive life-history traits in an annual weed. *New Phytologist* **184**: 806–818.
- Cano, L., Escarre, J., Fleck, I. et al. (2008). Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio pterophorus*. *Journal of Ecology* **96**: 468–476.

- Chown, S.L., Hodgins, K.A., Griffin, P.C. et al. (2015). Biological invasions, climate change and genomics. *Evolutionary Applications* **8**: 23–46.
- Chun, Y.J. (2011). Phenotypic plasticity of introduced versus native purple loosestrife: univariate and multivariate reaction norm approaches. *Biological Invasions* **13**: 819–829.
- Colautti, R.I. and Barrett, S.C.H. (2010). Natural selection and genetic constraints on flowering phenology in an invasive plant. *International Journal of Plant Sciences* **171**: 960–971.
- Colautti, R.I. and Barrett, S.C.H. (2013). Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* **342**: 364–366.
- Colautti, R.I. and Lau, J.A. (2015). Contemporary evolution during invasion: evidence for differentiation, natural selection, and local adaptation. *Molecular Ecology* **24**: 1999–2017.
- Colautti, R.I., Ricciardi, A., Grigorovich, I.A., and MacIsaac, H.J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecology Letters* **7**: 721–733.
- Colautti, R.I., Maron, J.L., and Barrett, S.C.H. (2009). Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications* **2**: 187–199.
- Colautti, R.I., White, N.A., and Barrett, S.C.H. (2010). Variation of self-incompatibility within invasive populations of purple loosestrife (*Lythrum salicaria* L.) from eastern North America. *International Journal of Plant Sciences* **171**: 158–166.
- Colomer-Ventura, F., Martínez-Vilalta, J., Zuccarini, P. et al. (2015). Contemporary evolution of an invasive plant is associated with climate but not with herbivory. *Functional Ecology* **29**: 1475–1485.
- Conte, G.L., Hodgins, K.A., Yeaman, S. et al. (2017). Bioinformatically predicted deleterious mutations reveal complementation in the interior spruce hybrid complex. *BMC Genomics* **18**: 970.
- Cook, S.A. and Johnson, M.P. (1968). Adaptation to heterogeneous environments. I. Variation in heterophylly in *Ranunculus flammula* L. *Evolution* **22**: 496–516.
- Corbi, J., Baack, E.J., Dechaine, J.M. et al. (2017). Genome-wide analysis of allele frequency change in sunflower crop-wild hybrid populations evolving under natural conditions. *Molecular Ecology* **27**: 233–247.
- Crawley, M. (1987). What makes a community invasible? In: *Colonization, Succession and Stability* (ed. A.J. Gray, M.J. Crawley and P.J. Edwards), 429–453. Oxford: Blackwell.
- Crispo, E. (2007). The Baldwin effect and genetic assimilation: revisiting two mechanisms of evolutionary change mediated by phenotypic plasticity. *Evolution* **61**: 2469–2479.
- Crooks, J.A. (2005). Lag times and exotic species: the ecology and management of biological invasions in slow-motion. *Ecoscience* **12**: 316–329.
- Cwynar, L.C. and MacDonald, G.M. (1987). Geographical variation of lodgepole pine in relation to population history. *American Naturalist* **12**: 40–48.
- Davidson, A.M., Jennions, M., and Nicotra, A.B. (2011). Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* **14**: 419–431.
- Davis, M.A., Grime, J.P., and Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**: 528–534.

- Dawson, W., Burslem, D.F.R.P., and Hulme, P.E. (2009). Factors explaining alien plant invasion success in a tropical ecosystem differ at each stage of invasion. *Journal of Ecology* **97**: 657–665.
- Delouche, J.C., Burgos, N.R., Gealy, D.R. et al. (2007). Seed shattering and dormancy in weedy rices. In: *Weedy Rices—Origin, Biology, Ecology and Control*, vol. 4, 19. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Dlugosch, K.M. and Parker, I.M. (2008). Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* **17**: 431–449.
- Dlugosch, K.M., Anderson, S.R., Braasch, J. et al. (2015a). The devil is in the details: genetic variation in introduced populations and its contributions to invasion. *Molecular Ecology* **24**: 2095–2111.
- Dlugosch, K.M., Cang, F.A., Barker, B.S. et al. (2015b). Evolution of invasiveness through increased resource use in a vacant niche. *Nature Plants* **1**: 15066.
- Doorduyn, L.J. and Vrieling, K. (2011). A review of the phytochemical support for the shifting defence hypothesis. *Phytochemistry Reviews* **10**: 99–106.
- Dostal, P. (2011). Plant competitive interactions and invasiveness: searching for the effects of phylogenetic relatedness and origin on competition intensity. *The American Naturalist* **177**: 655–667.
- Dytham, C. (2009). Evolved dispersal strategies at range margins. *Proceedings of the Royal Society B: Biological Sciences* **276**: 1407–1413.
- Ellstrand, N.C. and Schierenbeck, K.A. (2000). Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences* **97**: 7043–7050.
- Ellstrand, N.C., Heredia, S.M., Leak-Garcia, J.A. et al. (2010). Crops gone wild: evolution of weeds and invasives from domesticated ancestors. *Evolutionary Applications* **3**: 494–504.
- Excoffier, L., Foll, M., and Petit, R.J. (2009). Genetic consequences of range expansions. *Annual Review of Ecology, Evolution, and Systematics* **40**: 481–501.
- Facon, B., Hufbauer, R.A., Tayeh, A. et al. (2011). Inbreeding depression is purged in the invasive insect *Harmonia axyridis*. *Current Biology* **21**: 424–427.
- Felker-Quinn, E., Schweitzer, J.A., and Bailey, J.K. (2013). Meta-analysis reveals evolution in invasive plant species but little support for evolution of increased competitive ability (EICA). *Ecology and Evolution* **3**: 739–751.
- Fox, C.W. and Reed, D.H. (2011). Inbreeding depression increases with environmental stress: an experimental study and meta-analysis. *Evolution* **65**: 246–258.
- Franks, S.J., Pratt, P.D., Dray, F.A., and Simms, E.L. (2008). Selection on herbivory resistance and growth rate in an invasive plant. *The American Naturalist* **171**: 678–691.
- Funk, J.L. (2008). Differences in plasticity between invasive and native plants from a low resource environment. *Journal of Ecology* **96**: 1162–1173.
- Gallien, L., Thuiller, W., Fort, N. et al. (2016). Is there any evidence for rapid, genetically-based, climatic niche expansion in the invasive common ragweed? *PLoS One* **11**: 1–17.
- Gaskin, J.F. (2017). The role of hybridization in facilitating tree invasion. *AoB PLANTS* **9**: plw079.
- Gilbert, K.J., Sharp, N.P., Angert, A.L. et al. (2017). Local adaptation interacts with expansion load during range expansion: maladaptation reduces expansion load. *The American Naturalist* **189**: 368–380.

- Godoy, O., Saldana, A., Fuentes, N. et al. (2011). Forests are not immune to plant invasions: phenotypic plasticity and local adaptation allow *Prunella vulgaris* to colonize a temperate evergreen rainforest. *Biological Invasions* **13**: 1615–1625.
- Gomulkiewicz, R., Holt, R.D., Barfield, M., and Nuismer, S.L. (2010). Genetics, adaptation, and invasion in harsh environments. *Evolutionary Applications* **3**: 97–108.
- González-Martínez, S.C., Ridout, K., and Pannell, J.R. (2017). Range expansion compromises adaptive evolution in an outcrossing plant. *Current Biology* **27**: 2544–2551.
- Grant, P.R. and Grant, B.R. (1995). Predicting microevolutionary responses to directional selection on heritable variation. *Evolution* **49**: 241–251.
- Grime, J. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**: 1169–1194.
- Grossenbacher, D.L., Brandvain, Y., Auld, J.R. et al. (2017). Self-compatibility is over-represented on islands. *New Phytologist* **215**: 469–478.
- Grotkopp, E. and Rejmanek, M. (2007). High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *American Journal of Botany* **94**: 526–532.
- Gruntman, M., Segev, U., Glauser, G., and Tielbörger, K. (2017). Evolution of plant defences along an invasion chronosequence: defence is lost due to enemy release – but not forever. *Journal of Ecology* **105**: 255–264.
- Hallatschek, O. and Nelson, D.R. (2009). Life at the front of an expanding population. *Evolution* **64**: 193–206.
- Hamilton, M.A., Murray, B.R., Cadotte, M.W. et al. (2005). Life history correlates of plant invasiveness at regional and continental scales. *Ecology Letters* **8**: 1066–1074.
- Hargreaves, A.L. and Eckert, C.G. (2014). Evolution of dispersal and mating systems along geographic gradients: implications for shifting ranges. *Functional Ecology* **28**: 5–21.
- He, W.-M., Thelen, G.C., Ridenour, W.M., and Callaway, R.M. (2010). Is there a risk to living large? Large size correlates with reduced growth when stressed for knapweed populations. *Biological Invasions* **12**: 3591–3598.
- Hegde, S.G., Nason, J.D., Clegg, J., and Ellstrand, N.C. (2006). The evolution of California's wild radish has resulted in the extinction of its progenitors. *Evolution* **60**: 1187–1197.
- Hendry, A.P. (2016). *Eco-evolutionary Dynamics*. Princeton, NJ: Princeton University Press.
- Hendry, A.P. and Kinnison, M.T. (1999). The pace of modern life: measuring rates of contemporary microevolution. *Evolution* **53**: 1637–1653.
- Henn, B.M., Botigué, L.R., Peischl, S. et al. (2016). Distance from sub-Saharan Africa predicts mutational load in diverse human genomes. *Proceedings of the National Academy of Sciences* **113**: E440–E449.
- Hodgins, K.A. and Rieseberg, L. (2011). Genetic differentiation in life-history traits of introduced and native common ragweed (*Ambrosia artemisiifolia*) populations. *Journal of Evolutionary Biology* **24**: 2731–2749.
- Hodgins, K.A., Bock, D.G., Hahn, M.A. et al. (2015). Comparative genomics in the Asteraceae reveals little evidence for parallel evolutionary change in invasive taxa. *Molecular Ecology* **24**: 2226–2240.

- Hollingsworth, M.L. and Bailey, J.P. (2000). Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knotweed). *Botanical Journal of the Linnean Society* **133**: 463–472.
- Hooftman, D.A.P., Jong, M.J.D., Oostermeijer, J.G.B., and Den Nijs, J.C.M. (2007). Modelling the long-term consequences of crop-wild relative hybridization: a case study using four generations of hybrids. *Journal of Applied Ecology* **44**: 1035–1045.
- Hovick, S.M. and Whitney, K.D. (2014). Hybridisation is associated with increased fecundity and size in invasive taxa: meta-analytic support for the hybridisation-invasion hypothesis. *Ecology Letters* **17**: 1464–1477.
- Huang, F. and Peng, S. (2016). Intraspecific competitive ability declines towards the edge of the expanding range of the invasive vine *Mikania micrantha*. *Oecologia* **181**: 115–123.
- Huang, F., Peng, S., Chen, B. et al. (2015). Rapid evolution of dispersal-related traits during range expansion of an invasive vine *Mikania micrantha*. *Oikos* **124**: 1023–1030.
- Huot, B., Yao, J., Montgomery, B.L., and He, S.Y. (2014). Growth-defense tradeoffs in plants: a balancing act to optimize fitness. *Molecular Plant* **7**: 1267–1287.
- Joshi, J. and Vrieling, K. (2005). The enemy release and EICA hypothesis revisited: Incorporating the fundamental difference between specialist and generalist herbivores. *Ecology Letters* **8**: 704–714.
- Joshi, S., Gruntman, M., Bilton, M. et al. (2014). A comprehensive test of evolutionarily increased competitive ability in a highly invasive plant species. *Annals of Botany* **114**: 1761–1768.
- Kane, N.C. and Rieseberg, L.H. (2008). Genetics and evolution of weedy *Helianthus annuus* populations: adaptation of an agricultural weed. *Molecular Ecology* **17**: 384–394.
- Karasov, T.L., Chae, E., Herman, J.J., and Bergelson, J. (2017). Mechanisms to mitigate the trade-off between growth and defense. *The Plant Cell* **29**: 666–680.
- Kaufman, S.R. and Smouse, P.E. (2001). Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. *Oecologia* **127**: 487–494.
- Keane, R. and Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* **17**: 164–170.
- Keller, S.R., Sowell, D.R., Neiman, M. et al. (2009). Adaptation and colonization history affect the evolution of clines in two introduced species. *The New Phytologist* **183**: 678–690.
- Kinnison, M.T. and Hendry, A.P. (2001). The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112–113**: 145–164.
- Kirkpatrick, M. and Jarne, P. (2000). The effects of a bottleneck on inbreeding depression and the genetic load. *American Naturalist* **155**: 154–167.
- van Kleunen, M. and Fischer, M. (2005). Constraints on the evolution of adaptive phenotypic plasticity in plants. *New Phytologist* **166**: 49–60.
- van Kleunen, M. and Johnson, S.D. (2007). Effects of self-compatibility on the distribution range of invasive European plants in North America. *Conservation Biology* **21**: 1537–1544.
- van Kleunen, M., Weber, E., and Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* **13**: 235–245.
- van Kleunen, M., Dawson, W., and Maurel, N. (2015). Characteristics of successful alien plants. *Molecular Ecology* **24**: 1954–1968.

- Klüber, A. and Eckert, C.G. (2005). Interaction between founder effect and selection during biological invasion in an aquatic plant. *Evolution* **59**: 1900–1913.
- Klopfstein, S., Currat, M., and Excoffier, L. (2006). The fate of mutations surfing on the wave of a range expansion. *Molecular Biology and Evolution* **23**: 482–490.
- Kolar, C.S. and Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution* **16**: 199–204.
- Kolbe, J.J., Leal, M., Schoener, T.W. et al. (2012). Founder effects persist despite adaptive differentiation: a field experiment with lizards. *Science* **335**: 1086–1089.
- Lachmuth, S., Durka, W., and Schurr, F.M. (2011). Differentiation of reproductive and competitive ability in the invaded range of *Senecio inaequidens*: the role of genetic Allee effects, adaptive and nonadaptive evolution. *New Phytologist* **192**: 529–541.
- Lake, J.C. and Lewisham, M.R. (2004). Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. *Biological Conservation* **117**: 215–226.
- Lande, R. (2009). Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* **22**: 1435–1446.
- Lande, R. (2014). Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. *Journal of Evolutionary Biology* **27**: 866–875.
- Lande, R. (2015). Evolution of phenotypic plasticity in colonizing species. *Molecular Ecology* **24**: 2038–2045.
- Lande, R. and Schemske, D.W. (1985). The evolution of self-fertilization and inbreeding depression in plants: I. Genetic models. *Evolution* **39**: 24–40.
- Leger, E.A. and Rice, K.J. (2003). Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* **6**: 257–264.
- Lehe, R., Hallatschek, O., and Peliti, L. (2012). The rate of beneficial mutations surfing on the wave of a range expansion. *PLoS Computational Biology* **8**: e1002447.
- Leishman, M.R., Haslehurst, T., Ares, A., and Baruch, Z. (2007). Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* **176**: 635–643.
- Lewontin, R. (1965). Selection for colonizing ability. In: *The Genetics of Colonizing Species* (ed. H. Baker and G. Stebbins), 77–94. New York: Academic Press.
- Li, X.M., Liao, W.J., Wolfe, L.M., and Zhang, D.Y. (2012). No evolutionary shift in the mating system of North American *Ambrosia artemisiifolia* (Asteraceae) following its introduction to China. *PLoS One* **7**: 1–6.
- Lloret, F., Medial, F., Brundu, G. et al. (2005). Species attributes and invasion success by alien plants on Mediterranean islands. *Journal of Ecology* **93**: 512–520.
- Lohmueller, K.E., Indap, A.R., Schmidt, S. et al. (2008). Proportionally more deleterious genetic variation in European than in African populations. *Nature* **451**: 994–998.
- Lombaert, E., Estoup, A., Facon, B. et al. (2014). Rapid increase in dispersal during range expansion in the invasive ladybird *Harmonia axyridis*. *Journal of Evolutionary Biology* **27**: 508–517.
- Londo, J.P. and Schaal, B.A. (2007). Origins and population genetics of weedy red rice in the USA. *Molecular Ecology* **16**: 4523–4535.
- Lowe, W.H., Kovach, R.P., and Allendorf, F.W. (2017). Population genetics and demography unite ecology and evolution. *Trends in Ecology & Evolution* **32**: 141–152.

- MacArthur, R.H. and Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Marchini, G.L., Sherlock, N.C., Ramakrishnan, A.P. et al. (2016). Rapid purging of genetic load in a metapopulation and consequences for range expansion in an invasive plant. *Biological Invasions* **18**: 183–196.
- Maron, J.L., Vilà, M., Bommarco, R. et al. (2004). Rapid evolution of an invasive plant. *Ecological Monographs* **74**: 261–280.
- Mesgarana, M.B., Lewis, M.A., Adesc, P.K. et al. (2016). Hybridization can facilitate species invasions, even without enhancing local adaptation. *Proceedings of the National Academy of Sciences* **113**: 10210–10214.
- Mole, S. (1994). Trade-offs and constraints in plant-herbivore defense theory: a life-history perspective. *Oikos* **71**: 3–12.
- Monty, A. and Mahy, G. (2010). Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae). *Oikos* **119**: 1563–1570.
- Moodley, D., Geerts, S., Richardson, D.M., and Wilson, J.R.U. (2013). Different traits determine introduction, naturalization and invasion success in woody plants: Proteaceae as a test case. *PLoS One* **8**: e75078.
- Moran, E.V., Reid, A., and Levine, J.M. (2017). Population genetics and adaptation to climate along elevation gradients in invasive *Solidago canadensis*. *PLoS One* **12**: e0185539.
- Moravcova, L., Pysek, P., Jarosik, V., and Pergl, J. (2015). Getting the right traits: reproductive and dispersal characteristics predict the invasiveness of herbaceous plant species. *PLoS One* **10**: e0123634.
- Müller-Schärer, H., Schaffner, U., and Steinger, T. (2004). Evolution in invasive plants: Implications for biological control. *Trends in Ecology & Evolution* **19**: 417–422.
- Murren, C.J., Maclean, H.J., Diamond, S.E. et al. (2014). Evolutionary change in continuous reaction norms. *American Naturalist* **183**: 453–467.
- Murren, C.J., Auld, J.R., Callahan, H. et al. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. *Heredity* **115**: 293–301.
- van Noordwijk, A. and de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *American Naturalist* **128**: 137–142.
- Ochocki, B.M. and Miller, T.E.X. (2017). Rapid evolution of dispersal ability makes biological invasions faster and more variable. *Nature Communications* **8**: 1–8.
- Oduor, A.M.O., Leimu, R., and van Kleunen, M. (2016). Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *Journal of Ecology* **104**: 957–968.
- Orians, C.M. (2000). The effects of hybridization in plants on secondary chemistry: implications for the ecology and evolution of plant–herbivore interactions. *American Journal of Botany* **87**: 1749–1756.
- Orians, C.M. and Ward, D. (2010). Evolution of plant defenses in nonindigenous environments. *Annual Review of Entomology* **55**: 439–459.
- Palacio-Lopez, K. and Gianoli, E. (2011). Invasive plants do not display greater phenotypic plasticity than their native or non-invasive counterparts: a meta-analysis. *Oikos* **120**: 1393–1401.
- Pandit, M.K., Pockock, M.J.O., and Kunin, W.E. (2011). Ploidy influences rarity and invasiveness in plants. *Journal of Ecology* **99**: 1108–1115.

- Pannell, J.R. (2015). Evolution of the mating system in colonizing plants. *Molecular Ecology* **24**: 2018–2037.
- Parepa, M., Fischer, M., Krebs, C., and Bossdorf, O. (2014). Hybridization increases invasive knotweed success. *Evolutionary Applications* **7**: 413–420.
- Payseur, B.A. and Rieseberg, L.H. (2016). A genomic perspective on hybridization and speciation. *Molecular Ecology* **25**: 2337–2360.
- Peischl, S. and Excoffier, L. (2015). Expansion load: recessive mutations and the role of standing genetic variation. *Molecular Ecology* **24**: 2084–2094.
- Peischl, S., Dupanloup, I., Kirkpatrick, M., and Excoffier, L. (2013). On the accumulation of deleterious mutations during range expansions. *Molecular Ecology* **22**: 5972–5982.
- Peischl, S., Kirkpatrick, M., and Excoffier, L. (2015). Expansion load and the evolutionary dynamics of a species range. *The American Naturalist* **185**: E81–E93.
- Peischl, S., Dupanloup, I., Bosshard, L., and Excoffier, L. (2016). Genetic surfing in human populations: from genes to genomes. *Current Opinion in Genetics and Development* **41**: 53–61.
- Perkins, T.A., Boettiger, C., and Phillips, B.L. (2016). After the games are over: life-history trade-offs drive dispersal attenuation following range expansion. *Ecology and Evolution* **6**: 6425–6434.
- Perrins, J., Williamson, M., and Fitter, A. (1992). Do annual weeds have predictable characters. *Acta Oecologica – International Journal of Ecology* **13**: 517–533.
- Petanidou, T., Godfree, R.C., Song, D.S. et al. (2012). Self-compatibility and plant invasiveness: comparing species in native and invasive ranges. *Perspectives in Plant Ecology, Evolution and Systematics* **14**: 3–12.
- Petitpierre, B., Kueffer, C., Broennimann, O. et al. (2012). Climatic niche shifts are rare among terrestrial plant invaders. *Science* **335**: 1344–1348.
- Pfennig, K.S., Kelly, A.L., and Pierce, A.A. (2016). Hybridization as a facilitator of species range expansion. *Proceedings of the Royal Society B: Biological Sciences* **283**: 20161329.
- Phillips, B.L. (2012). Range shift promotes the formation of stable range edges. *Journal of Biogeography* **39**: 153–161.
- Phillips, B.L. (2015). Evolutionary processes make invasion speed difficult to predict. *Biological Invasions* **17**: 1949–1960.
- Phillips, B.L., Brown, G.P., Webb, J.K., and Shine, R. (2006). Invasion and the evolution of speed in toads. *Nature* **439**: 803.
- Phillips, B.L., Brown, G.P., Travis, J.M.J., and Shine, R. (2008). Reid's paradox revisited: the evolution of dispersal kernels during range expansion. *The American Naturalist* **172**: S34–S48.
- Phillips, B.L., Brown, G.P., and Shine, R. (2010). Evolutionarily accelerated invasions: the rate of dispersal evolves upwards during the range advance of cane toads. *Journal of Evolutionary Biology* **23**: 2595–2601.
- Pujol, B., Zhou, S.-R.R., Sanchez Vilas, J. et al. (2009). Reduced inbreeding depression after species range expansion. *Proceedings of the National Academy of Sciences of the United States of America* **106**: 15379–15383.
- Pysek, P. (1997). Clonality and plant invasions: can a trait make a difference? In: *The Ecology and Evolution of Clonal Plants* (ed. H. de Kroon and J. van Groenendael), 405–427. Leiden: Backhuys Publishers.

- Pysek, P. and Richardson, D.M. (2007). Traits associated with invasiveness in alien plants: where do we stand? In: *Biological Invasions, Ecological Studies*, vol. **193** (ed. W. Nentwig), 97–125. Berlin & Heidelberg: Springer-Verlag.
- Pysek, P., Prach, K., and Smilauer, P. (1995). Relating invasion success to plant traits: an analysis of the Czech alien flora. In: *Plant Invasions – General Aspects and Special Problems* (ed. P. Pysek, K. Prach, M. Rejmanek and M. Wade), 39–60. Amsterdam: SPB Academic Publishing.
- Pysek, P., Sadlo, J., Mandak, B., and Jarosik, V. (2003). Czech alien flora and the historical pattern of its formation: what came first to Central Europe? *Oecologia* **135**: 122–130.
- Rambuda, T.D. and Johnson, S.D. (2004). Breeding systems of invasive alien plants in South Africa: does Baker's rule apply? *Diversity & Distributions* **10**: 409–416.
- Reich, P.B., Walters, M.B., and Ellsworth, D.S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the United States of America* **94**: 13730–13734.
- Reichard, S. and White, P. (2001). Horticulture as a pathway of invasive plant introductions in the United States. *Bioscience* **51**: 103–113.
- Rejmanek, M. (1996). A theory of seed plant invasiveness: the first sketch. *Biological Conservation* **78**: 171–181.
- Rejmanek, M. and Richardson, D.M. (1996). What attributes make some plant species more invasive? *Ecology* **77**: 1655–1661.
- Richards, C.L., Bossdorf, O., Muth, N.Z. et al. (2006). Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* **9**: 981–993.
- Richardson, D.M. and Pyšek, P. (2006). Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* **30**: 409–431.
- Rieseberg, L.H. and Ellstrand, N.C. (1993). What can morphological and molecular markers tell us about plant hybridization? *Critical Reviews in Plant Sciences* **12**: 213–241.
- Rieseberg, L.H., Archer, M.A., and Wayne, R.K. (1999). Transgressive segregation, adaptation, and speciation. *Heredity* **83**: 363–372.
- Rius, M. and Darling, J.A. (2014). How important is intraspecific genetic admixture to the success of colonising populations? *Trends in Ecology & Evolution* **29**: 233–242.
- Samis, K.E., Murren, C.J., Bossdorf, O. et al. (2012). Longitudinal trends in climate drive flowering time clines in North American *Arabidopsis thaliana*. *Ecology and Evolution* **2**: 1162–1180.
- Schierenbeck, K.A. and Ellstrand, N.C. (2009). Hybridization and the evolution of invasiveness in plants and other organisms. *Biological Invasions* **11**: 1093–1105.
- Schlichting, C.D. (1986). The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* **17**: 667–693.
- Schlichting, C.D. (2008). Hidden reaction norms, cryptic genetic variation, and evolvability. *Annals of the New York Academy of Sciences* **1133**: 187–203.
- Schlichting, C.D. and Levin, D.A. (1988). Phenotypic plasticity in *Phlox*. I. Wild and cultivated populations of *P. drummondii*. *American Journal of Botany* **75**: 161–169.
- Schrieber, K. and Lachmuth, S. (2016). The genetic paradox of invasions revisited: the potential role of inbreeding × environment interactions in invasion success. *Biological Reviews* **91**: 939–952.

- Schrieber, K., Wolf, S., Wypior, C. et al. (2017). Adaptive and non-adaptive evolution of trait means and genetic trait correlations for herbivory resistance and performance in an invasive plant. *Oikos* **126**: 572–582.
- Shine, R., Brown, G.P., and Phillips, B.L. (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences* **108**: 5708–5711.
- Siemann, E., DeWalt, S.J., Zou, J., and Rogers, W.E. (2016). An experimental test of the EICA hypothesis in multiple ranges: invasive populations outperform those from the native range independent of insect herbivore suppression. *AoB Plants* **9**: plw087.
- Simmons, A.D. and Thomas, C.D. (2004). Changes in dispersal during species' range expansions. *American Naturalist* **164**: 378–395.
- Simons, Y.B., Turchin, M.C., Pritchard, J.K., and Sella, G. (2014). The deleterious mutation load is insensitive to recent population history. *Nature Genetics* **46**: 220–224.
- Snow, A.A. and Campbell, L.G. (2005). Can feral radishes become weeds? In: *Crop Fertility and Volunteerism* (ed. J. Gressel), 193–208. Boca Raton, FL: CRC Press.
- Stelkens, R. and Seehausen, O. (2009). Genetic distance between species predicts novel trait expression in their hybrids. *Evolution* **63**: 884–897.
- Stelkens, R.B., Brockhurst, M.A., Hurst, G.D.D., and Greig, D. (2014). Hybridization facilitates evolutionary rescue. *Evolutionary Applications* **7**: 1209–1217.
- Stock, A.J., Campitelli, B.E., and Stinchcombe, J.R. (2014). Quantitative genetic variance and multivariate clines in the Ivyleaf morning glory, *Ipomoea hederacea*. *Philosophical Transactions of the Royal Society B: Biological Sciences* **369**: 20130259.
- Strauss, S.Y., Rudgers, J.A., Lau, J.A., and Irwin, R.E. (2002). Direct and ecological costs of resistance to herbivory. *Trends in Ecology and Evolution* **17**: 278–285.
- Tabassum, S. and Leishman, M.R. (2018). Have your cake and eat it too: greater dispersal ability and faster germination towards range edges of an invasive plant species in eastern Australia. *Biological Invasions* **20**: 1199–1210.
- Thurber, C.S., Reagon, M., Gross, B.L. et al. (2010). Molecular evolution of shattering loci in U.S. weedy rice. *Molecular Ecology* **19**: 3271–3284.
- Todesco, M., Pascual, M.A., Owens, G.L. et al. (2016). Hybridization and extinction. *Evolutionary Applications* **9**: 892–908.
- Travis, J.M.J. and Dytham, C. (2002). Dispersal evolution during invasions. *Evolutionary Ecology Research* **4**: 1119–1129.
- Travis, J.M.J., Münkemüller, T., Burton, O.J. et al. (2007). Deleterious mutations can surf to high densities on the wave front of an expanding population. *Molecular Biology and Evolution* **24**: 2334–2343.
- Travis, J.M.J., Mustin, K., Benton, T.G., and Dytham, C. (2009). Accelerating invasion rates result from the evolution of density-dependent dispersal. *Journal of Theoretical Biology* **259**: 151–158.
- Turner, K.G., Hufbauer, R.A., and Rieseberg, L.H. (2014). Rapid evolution of an invasive weed. *The New Phytologist* **202**: 309–321.
- Turner, K.G., Fréville, H., and Rieseberg, L.H. (2015). Adaptive plasticity and niche expansion in an invasive thistle. *Ecology and Evolution* **5**: 3183–3197.
- Uesugi, A., Connallon, T., Kessler, A., and Monro, K. (2017). Relaxation of herbivore-mediated selection drives the evolution of genetic covariances between plant competitive and defense traits. *Evolution* **71**: 1700–1709.
- Uller, T. and Leimu, R. (2011). Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology* **17**: 3478–3485.

- Vila, M. and D'Antonio, C.M. (1998). Hybrid vigor for clonal growth in *Carpobrotus* (Aizoaceae) in coastal California. *Ecological Applications* **8**: 1196–1205.
- Waddington, C.H. (1953). Genetic assimilation of an acquired character. *Evolution* **7**: 118–126.
- Weiss-Lehman, C., Hufbauer, R.A., and Melbourne, B.A. (2017). Rapid trait evolution drives increased speed and variance in experimental range expansions. *Nature Communications* **8**: 1–7.
- Whitney, K.D., Randell, R.A., and Rieseberg, L.H. (2006). Adaptive introgression of herbivore resistance traits in the weedy sunflower *Helianthus annuus*. *American Naturalist* **167**: 794–807.
- Whitney, K.D., Ahern, J.R., and Campbell, L.G. (2009). Hybridization-prone plant families do not generate more invasive species. *Biological Invasions* **11**: 1205–1215.
- Williams, J.L., Kendall, B.E., and Levine, J.M. (2016a). Rapid evolution accelerates plant population spread in fragmented experimental landscapes. *Science* **353**: 482–486.
- Williams, J.L., Snyder, R.E., and Levine, J.M. (2016b). The influence of evolution on population spread through patchy landscapes. *The American Naturalist* **188**: 15–26.
- Williamson, M. (1999). Invasions. *Ecography* **22**: 5–12.
- Williamson, M.H. and Fitter, A. (1996). The characters of successful invaders. *Biological Conservation* **78**: 163–170.
- Wright, S. (1931). Evolution in Mendelian populations. *Genetics* **16**: 97–159.
- Yang, J., Mezouk, S., Baumgarten, A. et al. (2017). Incomplete dominance of deleterious alleles contributes substantially to trait variation and heterosis in maize. *PLoS Genetics* **13**: e1007019.
- Yeaman, S., Hodgins, K.A., Lotterhos, K.E. et al. (2016). Convergent local adaptation to climate in distantly related conifers. *Science* **353**: 1431–1433.
- Züst, T. and Agrawal, A.A. (2017). Trade-offs between plant growth and defense against insect herbivory: an emerging mechanistic synthesis. *Annual Review of Plant Biology* **68**: 513–534.
- Züst, T., Rasmann, S., and Agrawal, A.A. (2015). Growth-defense tradeoffs for two major anti-herbivore traits of the common milkweed *Asclepias syriaca*. *Oikos* **124**: 1404–1415.