

FORUM

Integrating trait- and niche-based approaches to assess contemporary evolution in alien plant species

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Summary

1. Two primary lines of indirect evidence for contemporary evolution in alien species are based on differences between native and introduced ranges in one or more functional traits or a shift in environmental niche. Although the integration of trait and environmental niche perspectives is increasingly recognised as a key to understanding the role of life-history evolution in range-shifting populations, there has been no attempt to bring together these perspectives on the contemporary evolution of alien plant species.

2. We develop a set of scenarios that contrast trait–environment relationships observed in the field for alien species in the native and introduced range, and explore how they might be shaped by contemporary evolution. In each case, the limitations of uniquely trait or environmental niche perspectives are highlighted. The scenarios are examined in relation to long-term trends in covariation between temperature and first flowering date of European plant species introduced into the USA. Support for four of the scenarios is found.

3. Field studies examining how species traits respond to environmental variation along natural gradients cannot by themselves distinguish relationships arising from genetic variation, phenotypic plasticity or genetic variation for such plasticity. This is best assessed by reciprocal transplant experiments. However, trait–environment relationships provide a basis for better targeted common garden studies that are more hypothesis driven and that pinpoint the traits of interest, ascertain the appropriate selection gradients and the range over which they need to be observed, as well as identify candidate species for further study.

4. *Synthesis.* The need to improve species distribution models through a better understanding of underlying ecological and evolutionary processes makes assessments of trait–environment relationships, in both the native and introduced ranges, significant. They are of paramount importance when explaining the differential success of alien plants in novel environments as well as when predicting the potential for future range shifts following introduction. The current paucity of such comparisons represents a significant gap in our understanding of biological invasions.

Key-words: biological invasions, enemy release, exotic, invasion ecology, local adaptation, niche conservatism, niche shifts, phenology, phenotypic plasticity, range expansion, weed

Introduction

Although originating from distant biomes, introduced plants often establish in new regions in sufficient abundance to reduce native plant and animal diversity, as well as alter ecosystem services (Gaertner *et al.* 2009; Kettenring & Adams 2011; Vilà *et al.* 2011; Pyšek *et al.* 2012). Yet, alien plants

are colonists of regions in which they did not evolve and to which they may be poorly adapted, encountering a suite of novel biotic and abiotic stresses and selection pressures (Fridley *et al.* 2007; Prentis *et al.* 2008). Consequently, most plant species introduced into a region fail to establish self-maintaining populations in the wild (Hulme 2012). Successful establishment demands that newly introduced species possess at least one of three key characteristics: they should be physiologically matched to the particular conditions of the recipient environment (Schlaepfer *et al.* 2010); display sufficient

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phenotypic plasticity to maintain fitness in a new environment (Richards *et al.* 2006; Hulme 2008) and/or be able to adapt rapidly to novel biotic and abiotic conditions (Whitney & Ghalambor 2008). Distinguishing among these requirements and determining their relative importance presents an important challenge to invasion biologists interested in the mechanisms governing invasion success.

The widespread use of the similarity in climate between the native and introduced range to predict the likelihood of alien species establishment emphasises the importance of having an adequate environmental match that reflects pre-existing life-history and physiological traits favouring acclimatisation to the environment of the recipient region (Jeschke & Strayer 2008). Phenotypic plasticity is viewed as another important attribute enabling colonisation of novel environments as it can broaden a population's niche breadth, and therefore, its range of potentially available resources (Richards *et al.* 2006; Nicotra *et al.* 2010). In addition, phenotypic plasticity may itself be selected to fit species to the particular demands of different environments and local adaptation may be accompanied by an increase, decrease or no change in plasticity (Thompson 1991). However, only adaptive plasticity that places populations close enough to a new phenotypic optimum for directional selection to act will predictably enhance fitness and result in adaptive evolution on ecological time-scales in new environments (Ghalambor *et al.* 2007). Thus, while environmental matching and phenotypic plasticity may be important in the initial establishment and persistence of an invader following introduction, longer-term spread over an expanded range may require adaptive differentiation among the diverse environments encountered (Allan & Pannell 2009; Keller *et al.* 2009).

Given the relatively short timescales involved, rapid adaptation in alien species is expected to arise from standing genetic variation rather than new mutation (Barrett & Schluter 2008). For example, escape from specialist natural enemies may lead to the contemporary evolution of increased competitive ability of alien plants and subsequent colonisation of new environments in the introduced range (Bossdorf *et al.* 2005). Contemporary evolution may be facilitated by multiple introductions that result in levels of genetic diversity that exceed those found in the native range and present considerable potential for rapid adaptation to novel environments (Dlugosch & Parker 2008; Wiens *et al.* 2009). Thus, following the introduction of an alien species, beneficial alleles may be more likely to be available at moderate frequencies, and even alleles with neutral or deleterious effects can become advantageous in novel environments (Barrett, Colautti & Eckert 2008; Prentis *et al.* 2008). Nevertheless, the high dispersal rates observed for alien plants in heterogeneous environments (Aikio, Duncan & Hulme 2010), as well as rapid range expansion (Pyšek & Hulme 2005), can hamper local adaptation as high gene flow among populations may constrain evolution (Hoffmann & Sgro 2011). Thus, knowledge of the likelihood and speed at which local adaptation evolves in alien plants will be particularly important for predicting future invasion scenarios, assessing how populations may respond to

novel environments, as well as for management practices when evolutionary changes enhance ecological opportunities and the potential to spread.

A variety of approaches have examined the potential for adaptation in alien plant species. However, two primary lines of indirect evidence based on differences between native and introduced ranges are usually involved: trait divergence and climatic niche shifts. Here, a trait refers to any morphological, physiological or phenological feature measurable at the individual level which impacts fitness indirectly via its effects on growth, reproduction and survival (Violle *et al.* 2007). Trait comparisons, contrasting one or more sites in both the native and introduced range, have either assessed one or a few plant attributes (e.g. seed size, fecundity) across natural populations of multiple species (Thebaud & Simberloff 2001; Mason *et al.* 2008), or examined physiological measures of performance (e.g. growth rate, photosynthetic efficiency) for populations of a single species reciprocally transplanted among common gardens (Bossdorf *et al.* 2005). Trait comparisons most often aim to test whether significant increases in the fitness components of alien phenotypes (e.g. due to an absence of natural enemies and/or competitors) or genotypes (e.g. evolution of increased competitive ability as a result of reduced investment in defence) occur in the introduced range (Hierro, Maron & Callaway 2005; van Kleunen *et al.* 2010).

More recently, observations of climatic niche shifts between the native and introduced range have been proposed as evidence for adaptation by alien species to novel environments (Pearman *et al.* 2008; Gallagher *et al.* 2010; Mandley *et al.* 2010). The use of climate-distribution relationships in the native range to project future distributions in a new region assumes environmental niches are conserved in both the native and introduced range (Colwell & Rangel 2009). As a result, where anomalies in projections of alien ranges occur such that a species is found to occur outside its predicted environmental niche, they have often been cited as evidence for evolutionary shifts in the environmental niche following introduction (Holt 2009). This may occur as a result of selection on environmentally matched genotypes that leads to a subsequent shift in the climate niche (Treier *et al.* 2009). Yet, an adaptive explanation may not be correct if alien species simply benefit from enemy release and expand their range in enemy-free space (Mitchell & Power 2003). It should also be borne in mind that climate variables (e.g. temperature, precipitation) only correspond to a few axes of the multidimensional Hutchinsonian niche, and that following introduction shifts may occur along biotic axes (e.g. regeneration, resource use, phenology) that also result in alien species trait shifts (Holt 2009).

To date, there has been no attempt to conceptually integrate the trait and environmental niche perspectives on the contemporary evolution of alien species. Trait- and niche-based approaches are increasingly recognised as a key to understand the role of life-history evolution in range-shifting populations, explain the success of alien species and predict the impacts of climate change on species distributions (Sexton *et al.* 2009; Phillips, Brown & Shine 2010; Wiens *et al.* 2010; Hoffmann &

Sgro 2011). Here, we explore how an explicit examination of trait–environment relationships along naturally occurring environmental gradients in both the native and introduced ranges can be used to derive clearer hypotheses regarding the potential role of environmental matching, phenotypic plasticity and/or local adaptation in the establishment of alien plants. While we acknowledge that such methods are largely correlative and require further experimentation to test for contemporary evolution, we emphasise their utility in informing subsequent approaches and illustrate their value in identifying the pitfalls of focusing upon either trait or environmental niche perspectives in isolation from one another.

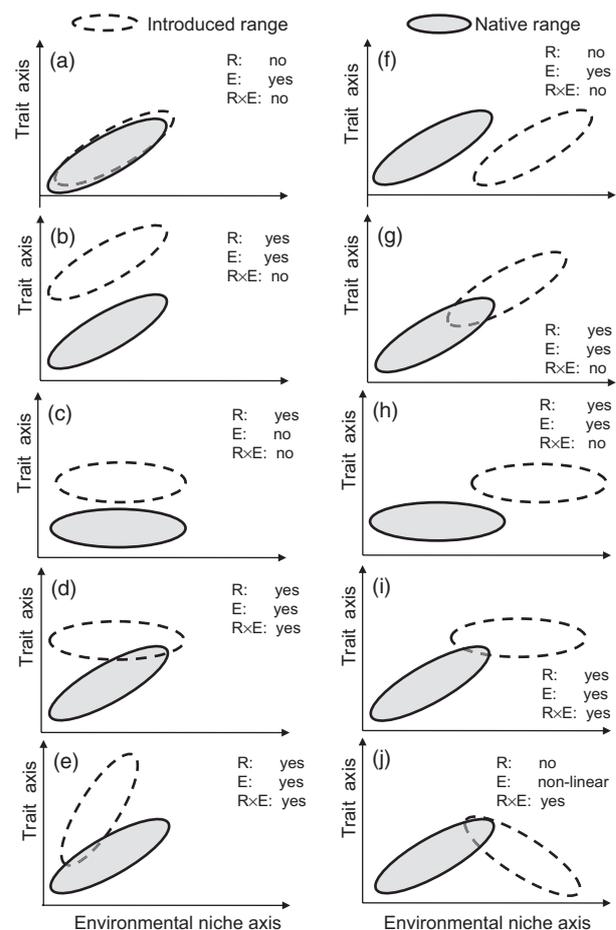
Using trait–environment relationships to study the contemporary evolution of alien species

Morphological (e.g. seed and leaf size), physiological (e.g. photosynthetic capacity) and phenological (e.g. floral initiation and duration) traits may show different attributes along environmental gradients or through time (Willis & Hulme 2004; Violle *et al.* 2007; Ross, Lambdon & Hulme 2008). An expected outcome of local adaptation is that traits and

Fig. 1. Schematic representation of the relationship between the value of a species trait (e.g. seed size, first flowering date, growth rate) and an environmental variable (e.g. temperature, precipitation, multivariate axis) characterising the abiotic niche of a hypothetical species sampled at multiple sites in both its native (shaded ellipse) and introduced (open ellipse) range. Illustrative examples of the outcome of analysis of covariance are provided to indicate whether the effect on trait values of the fixed factor Range (R, native or introduced), a covariate representing an Environmental gradient (E) or their interaction (R×E) would be significant: (a) trait–environment relationships are equivalent, neither the mean trait values nor the extent of the environmental gradient occupied by the species differ significantly between the native and introduced range and no significant interaction between the two variables occurs; (b) species traits are significantly correlated with the environmental gradient, but although species occur across a similar environmental gradient in both the native and introduced range, they exhibit significantly different mean trait values; (c) as in (b) but species traits are not significantly correlated with the environmental gradient; (d) the extent of the environmental gradient occupied by the species is similar between the native and introduced range, but both the mean trait values and environment relationships differ such that there would be a significant interaction between the two variables; (e) plants may respond to the local environmental gradient in both the native and introduced range but exhibit a different relationship with the environmental axis such that a difference in mean trait values between ranges is found; (f) a species occupies a different part of the environmental gradient in the introduced and native range but trait values change similarly with change in the environment in the two ranges; (g) mean trait values differ and the species is found to occupy a different region of the environmental gradient in the native compared with the introduced range but the overall significant relationship between the environment and trait values is similar and simply extended into a new environmental region; (h) as in (g) but the relationship between traits and environment is non-significant; (i) trait–environment relationships are asymptotic and are not extended in the introduced range; (j) trait–environment relationships are unimodal and the native range only samples a proportion of the potentially suitable environmental space and the introduced range extends the species environment space beyond the optimum for the particular trait examined.

environments covary (Kawecki & Ebert 2004). Therefore, examining whether such covariance is similar between native and introduced ranges should provide insights into the circumstances where contemporary evolution might occur. There are several circumstances where examination of trait–environment relationships between the native and introduced range provide different perspectives on contemporary evolution in alien species than might be gleaned solely from the study of differences in mean trait values or abiotic environmental niches (e.g. climatic variables). A total of 16 possible scenarios may be envisaged arising through differences between the native and introduced range in the slope of the trait–environment relationship, mean trait value, position along the environmental gradient, or a combination of two or more of these changes. For brevity and to avoid repetition, we focus on a subset of ten (Fig. 1).

We first explore the situation where a species occupies a similar position along an environmental gradient, reflecting analogous environmental niches, in both the native and introduced range. Where the relationship between a trait value and an environmental variable is equivalent (positive, negative or non-significant) in the native and introduced range, neither the mean trait values nor the location along the environmental gradient occupied by the species would differ significantly between ranges, and there would be no significant interaction between the two variables (Fig. 1a). Trait or environmental



niche perspectives based on population means would therefore conclude no evidence for contemporary evolution in alien species. Such a scenario is probable in cases where, due to phylogenetic and biogeographic constraints, natural communities do not contain the full range of life-forms observed globally, and this provides an opportunity that a species that has arisen elsewhere, even on another continent, may be environmentally matched to that physical environment (Mack 2003). The rising intentional and unintentional movement of species by humans through trade, transport and tourism increases the probability that introduced species will encounter environments similar to their native region to which they are environmentally matched (Hulme *et al.* 2008). The European vernal herb, garlic mustard (*Alliaria petiolata*), achieves high maximum rates of photosynthesis in early spring, and this promotes invasion of the deciduous forests of Eastern North America because at this time, many native ground layer species are still dormant (Myers & Anderson 2003). Nevertheless, parallel clinal variation in species attributes observed when multiple plant populations are sampled from across a wide latitudinal or altitudinal distribution in both the introduced and native range could be indicative of potential local adaptation. To examine this possibility, comparison of trait–environment relationships between the native and introduced range would be essential to assess whether plants are responding similarly to environmental controls in both ranges. However, such potential can only be confirmed if plants from both the introduced and native range continue to exhibit local differentiation when grown in a common garden environment. To date, such studies have consistently found evidence that native and alien genotypes have independently adapted to broad-scale variation in climate (Jakobs, Weber & Edwards 2004; Leger & Rice 2007; Maron, Elmdorf & Vilà 2007; Etterson *et al.* 2008; Alexander *et al.* 2009).

Species may occupy the same position along an environmental gradient in both the native and introduced range but exhibit significantly different mean trait values even though the slope of the relationship is similar and could either be significantly different from zero (Fig. 1b) or not (Fig. 1c). Increased performance, be it growth rate, plant biomass or fecundity, is expected following the introduction of a species to a new region where it benefits from the release of negative impacts from native natural enemies (Keane & Crawley 2002). However, evidence in support of such an expectation is mixed and differences in performance between native and introduced ranges may arise for a number of reasons that are not necessarily adaptive (Colautti *et al.* 2004). Furthermore, significant differences in mean trait values may not be due to adaptation but may arise through nonrandom sampling of the trait spectrum in the native range (Simons 2003), postintroduction genetic drift and founder effects (Dlugosch & Parker 2008), or hidden biogeographic biases (e.g. plants from the native and alien range are drawn from different latitudes and thus perform differently), and these may confound inferences about the causes of evolutionary change in alien plants (Colautti, Maron & Barrett 2009). Comparisons of traits sampled across a broad environmental gradient representative

of a species' distribution in both the native and introduced range can diminish the risk of sampling artefacts and provide a means to control for founder effects (Keller & Taylor 2008), as well as ensure biogeographic biases, such as latitude, are explicitly accounted for in subsequent analyses.

In each of the scenarios described above, the potential exists for a difference in slope to be found between the introduced and native range and in some cases this could indicate contemporary evolution. In the first instance, mean trait values and the environmental gradient occupied by the species may be similar between the native and introduced range, but the trait–environment relationships may differ such that there would be a significant interaction between the two variables. Slopes may differ where plants in the introduced region have not adapted to the local environmental gradient and clinal variation in potentially adaptive traits would be weak or absent (Fig. 1d). For example, where environmental matching is important in colonisation, multiple introductions from different source environments can lead to a mosaic of maladaptation where trait values in one population might be better suited to another environment (Dlugosch & Parker 2008). Alternatively, plants may adapt to the local environment but exhibit a different relationship with the environmental axis, which might occur as a result of enemy release that allows reallocation of resources and an altered trait–environment relationship (Fig. 1e). These differences would not be evident from a comparison of environmental niches or mean trait values alone and could even be missed in common garden studies if an insufficient range of environments is examined.

Although most approaches to alien species risk assessment assume a species will occupy a similar position along an environmental gradient in its native and introduced range, an increasing number of studies reveal that this is not the case (Hulme 2012). Shifts in the environmental tolerance of a species following introduction into a novel environment could result in species exhibiting similar mean trait values across a different environmental range (Fig. 1f). Evidence exists for differences in cold (Milne & Abbott 2000) and drought (Hodgins & Rieseberg 2011) tolerance when plant species are compared in both their native and introduced range. Although shifts in environmental tolerance may arise through local adaptation (Skalova, Moravcova & Pyšek 2011), such difference can also occur through shifts in cytotype frequency (Treier *et al.* 2009), hybridization (Milne & Abbott 2000) or trade-offs with another life-history trait that might itself be under selection and potentially show local adaptation, for example, growth rate (Hodgins & Rieseberg 2011).

Where a species occupies a distinct abiotic environmental niche in its introduced compared with its native range, traits might also be expected to differ. Not accounting for differences in environmental niche when comparing traits can significantly bias results towards interpreting trait differences as being the result of contemporary evolution. For example, the performance of plants grown in common garden experiments has been shown to be a function of the latitude from which the provenances were sampled such that differences in traits between the native and introduced regions may largely reflect

variation in the latitudinal ranges sampled in each region (this error was found in 10 of 32 studies examined by Colautti, Maron & Barrett 2009). Where mean trait values differ and the species is found to occupy different positions along an environmental gradient in the native and introduced range, both trait and environmental niche approaches might interpret such patterns as evidence for contemporary evolution. This could occur independently of whether the trait–environment relationship is significant (Fig. 1g) or not (Fig. 1h). While this pattern is consistent with contemporary evolution, it is also consistent with scenarios that do not involve the evolution of local adaptation. Indeed, such a shift could simply arise as a result of ecological fitting (Agosta & Klemens 2008), the process whereby organisms colonise and persist in novel environments, use different resources or form new associations with other species as a result of the suites of traits that they carry at the time they encounter the novel condition. For example, a species' environmental niche space (and hence trait variation) in its native range may be constrained by geographic barriers, dispersal limitation or biotic interactions (Brown, Stevens & Kaufman 1996). Once released from these constraints through human-mediated dispersal either across historical geographic barriers and/or to locations free from competitors and natural enemies, a species may extend its environmental niche space in the introduced range into regions for which there is no analogue in its native range.

Geographic barriers to dispersal probably explain why the narrow endemic, Canary Island St. John's wort (*Hypericum canariense*), has successfully established in a variety of regions worldwide encompassing a much wider range of environments than occur in its native range (Dlugosch & Parker 2007). However, it should be noted that even in the absence of geographic barriers, many native plants may not be at equilibrium with the environment, especially where their ranges continue to exhibit post-glacial expansion (Davis & Shaw 2001; Svenning & Skov 2007). Thus, it is not surprising that data from native ranges on their own are often insufficient to predict species distributions elsewhere (Broennimann & Guisan 2008). This implies that observed anomalies in range projections from species distribution models should not be used as robust evidence for adaptive niche shifts in the introduced range (Wiens *et al.* 2009). To date, there have been no comparative studies of plant species fitness components between the native and introduced range where the latter is believed to be the result of a climatic niche shift, but these are essential to distinguish between contemporary evolution and ecological fitting. To do this would require quantifying the match between the realised climatic niche and the distribution in the introduced and native ranges, to assess if a species occurred in climatic conditions outside those it occupied in its native range (Gallagher *et al.* 2010). Those species found to occur under 'novel' climate conditions would then be the subject of comparative performance studies examining trait–environment relationships in both the introduced and native range prior to further examination using reciprocal transplants in common garden experiments.

Two further scenarios illustrate patterns that may be observed when trait–environment relationships differ between the native and introduced range. A trait that varies with the environmental gradient in the native range may level off in the extended (or novel) environment experienced in the introduced range (Fig. 1i). This may occur if traits are limited to an upper value due to genetic, physiological and/or morphological constraints (Colautti, Eckert & Barrett 2010) even when faced with a potentially better environment (due to an absence of natural enemies or competitors). Where trait–environment relationships are unimodal (Willis & Hulme 2002; Dell, Pawar & Savage 2011) and the native range only samples a proportion of the potentially suitable environmental space, a species distribution in the introduced range may simply extend the species environment space beyond the optimum for the particular trait examined (Fig. 1j). This would result in a different trait–environment relationship in the introduced range. Under this scenario, an analysis based on mean trait values may not find evidence for contemporary evolution, but the observed environmental niche shift might be interpreted as adaptive. However, additional studies would be required to provide evidence for adaptation because ecological fitting may also result in an alien species occupying a distinct environment to its native range but still exhibit similar mean trait values.

Phenology–environment relationships in native and introduced plant populations

Long-term data on flowering phenology of the same taxa in North America and the United Kingdom can be used to illustrate the utility of explicitly comparing trait–environment relationships in the native and introduced ranges of plants. Details of the locations, species and analytical methods have been published elsewhere (Hulme 2011a) and are thus only briefly summarised here. Records of the first flowering date (FFD) of 19 European vascular species have been collated on an almost annual basis between 1970 and 2000 in both Washington, DC and Oxfordshire. In both regions, there has been progressive climate warming since 1970 and in most cases species show a similar marked advance in FFD (e.g. earlier flowering) with increasing winter/spring minimum temperatures (Hulme 2011a). Although flowering phenology is a key reproductive trait, with earlier flowering having the potential to confer a selective advantage by increasing the length of the flowering period, presenting greater opportunities for pollen dispersal and longer fruit maturation times, it has only rarely been examined in the light of alien plant success in novel environments (Hulme 2011b). However, we note that our example does differ from approaches that examine covariation in traits and environments across multiple populations in space along an environmental gradient because variation in phenology of the same populations between time periods is more likely to reflect pre-existing phenotypic plasticity rather than adaptive evolutionary change. However, broad-scale difference between locations over the entire sampling period may reflect contemporary evolution. Furthermore, our

example illustrates that trait–environment relationships do not necessarily require data from multiple sites across an environmental gradient but can be drawn from individual sites across multiple time periods.

Four classes of trait–environment comparisons were observed when examined individually for each of the 19 species and these map onto previously hypothesised scenarios (Fig. 1). For each species, results of GLM with FFD as the dependent variable, region (UK vs. USA) as a fixed factor and minimum winter temperature as a covariate are presented (Table 1) and illustrated for representative species (Fig. 2). Although Washington, DC experienced significantly lower mean winter/spring minimum temperatures (1.93 ± 0.17 °C) than Oxfordshire (3.14 ± 0.14 °C) over the 30-year period, interannual variability led to considerable overlap in the temperatures experienced in the native and introduced range (Hulme 2011a). Thus, the responses in FFD were observed over a largely similar environmental gradient, and there is no evidence that the species were occupying a distinct climate space in the introduced range (Fig. 2). The majority of species exhibited similar relationships between FFD and temperature in both Oxfordshire and Washington, DC. In four species (*Cardamine hirsuta*, *Plantago lanceolata*, *Ranunculus bulbosus*, *Tussilago farfara*), there was a significant environment effect (E) with lower minimum temperatures leading to later flowering, but the relationship was similar in each continent and there was no range (R) or range–environment (R×E) interaction (Fig. 2a, Table 1). However, the most common finding (eight species, Table 1) was that while the slope of the relationship between temperature and FFD was similar in both continents (significant E effect), species in Washington,

DC flowered several days earlier for a given minimum temperature (significant R effect but no R×E interaction, Fig. 2b). A further four species (*Achillea millefolium*, *Ajuga reptans*, *Cichorium intybus*, *Melilotus officinalis*) revealed no relationship between FFD and temperature (no E effect) in either range but again species in Washington, DC flowered several days earlier for a given minimum temperature (significant R effect but no R×E interaction, Fig. 2c). The earlier flowering in Washington, DC was most evident in species that flowered in the summer rather than the spring. This result is best explained by these species being able to respond more markedly to stronger vernalisation over the significantly colder winter period (Hulme 2011a). In addition, species that already flower early have less scope to advance FFD in relation to warming, as other non-temperature-dependent constraints such as photoperiod prevent winter flowering. Only three species (*Rumex acetosella*, *Chelidonium majus* and *Glechoma hederacea*) did not display consistent flowering responses between continents (significant R×E interaction, Fig. 2d). In each case, the species still tended to flower earlier in Washington, DC (significant R effect) but revealed a lack of temperature responsiveness in FFD in Washington, DC, in contrast to the finding that warming significantly advanced flowering in Oxfordshire (significant E effect). The three species have all been introduced into North America more than 200 years ago, and thus should have had sufficient time to adapt to the local environment. A lack of responsiveness in FFD to warming is not unusual (Fig. 2c), but can disadvantage species in their ability to respond to climate change (Hulme 2011b). An initial absence of temperature responsiveness in the introduced range is unlikely to be adaptive.

Table 1. Results of GLM with first flowering date (FFD) as the dependent variable (range (UK vs. USA) as a fixed factor and minimum winter temperature as a covariate for 19 species

Species	Oxford			Washington			P value		
	n	Slope	Intercept	n	Slope	Intercept	R	E	R×E
<i>Achillea millefolium</i>	23	-2.82 ± 2.96	178.08 ± 9.74	22	-3.64 ± 2.02	146.35 ± 4.36	0.003	0.077	0.818
<i>Ajuga reptans</i>	29	-0.57 ± 3.38	132.97 ± 10.96	21	-1.91 ± 2.75	104.95 ± 5.73	0.025	0.592	0.772
<i>Alliaria petiolata</i>	27	-7.39 ± 1.64	129.46 ± 5.29	26	-3.93 ± 1.34	110.13 ± 3.01	0.003	< 0.001	0.114
<i>Anthoxanthum odoratum</i>	20	-7.68 ± 3.47	147.70 ± 11.45	22	-4.99 ± 1.57	114.52 ± 3.50	0.003	0.001	0.457
<i>Barbarea vulgaris</i>	28	-3.57 ± 1.99	137.90 ± 6.41	25	-2.66 ± 1.42	106.59 ± 3.10	< 0.001	0.013	0.709
<i>Cardamine hirsuta</i>	27	-19.52 ± 4.98	112.61 ± 15.85	29	-16.64 ± 4.29	80.95 ± 9.26	0.100	< 0.001	0.667
<i>Chelidonium majus</i>	29	-7.93 ± 2.12	149.24 ± 6.82	21	+ 0.11 ± 1.82	111.58 ± 4.05	< 0.001	0.009	0.007
<i>Cichorium intybus</i>	17	+ 1.57 ± 3.62	184.00 ± 12.27	22	-2.46 ± 1.54	145.58 ± 3.46	0.001	0.808	0.272
<i>Galium aparine</i>	30	-5.94 ± 2.24	150.67 ± 7.25	24	-2.46 ± 1.91	121.33 ± 4.07	0.001	0.006	0.243
<i>Glechoma hederacea</i>	30	-11.71 ± 1.86	128.21 ± 6.04	28	-2.92 ± 2.22	92.98 ± 4.73	< 0.001	< 0.001	0.004
<i>Melilotus officinalis</i>	22	-2.30 ± 2.26	175.18 ± 6.97	22	+ 0.93 ± 1.49	131.69 ± 3.34	< 0.001	0.607	0.231
<i>Plantago lanceolata</i>	25	-7.32 ± 2.43	139.06 ± 7.77	23	-6.58 ± 1.49	130.81 ± 3.37	0.307	< 0.001	0.798
<i>Ranunculus bulbosus</i>	29	-15.30 ± 3.49	153.46 ± 11.23	24	-17.19 ± 3.50	153.46 ± 11.23	0.240	< 0.001	0.703
<i>Rumex acetosella</i>	20	-8.27 ± 1.86	159.32 ± 6.23	23	-1.16 ± 2.51	116.64 ± 5.67	< 0.001	0.007	0.036
<i>Rumex crispus</i>	28	-7.16 ± 2.68	173.92 ± 8.60	21	-5.23 ± 2.11	141.58 ± 4.64	0.001	0.001	0.577
<i>Solanum dulcamara</i>	24	-4.86 ± 2.55	166.43 ± 7.96	20	-3.86 ± 1.94	137.81 ± 4.21	0.002	0.011	0.761
<i>Trifolium pratense</i>	19	-2.87 ± 2.11	144.99 ± 6.59	24	-2.97 ± 1.27	125.37 ± 2.74	0.006	0.018	0.965
<i>Tussilago farfara</i>	30	-12.19 ± 3.36	97.44 ± 10.82	26	-8.27 ± 3.00	87.37 ± 6.16	0.418	< 0.001	0.388
<i>Veronica hederifolia</i>	28	-14.73 ± 3.30	118.50 ± 10.57	24	-6.63 ± 2.91	86.86 ± 6.22	0.013	< 0.001	0.072

Regression parameters (and their standard error) are provided for Oxfordshire and Washington, DC and the significance of range (R), temperature (E) and their interactions in GLM is presented and significant values highlighted in bold face.

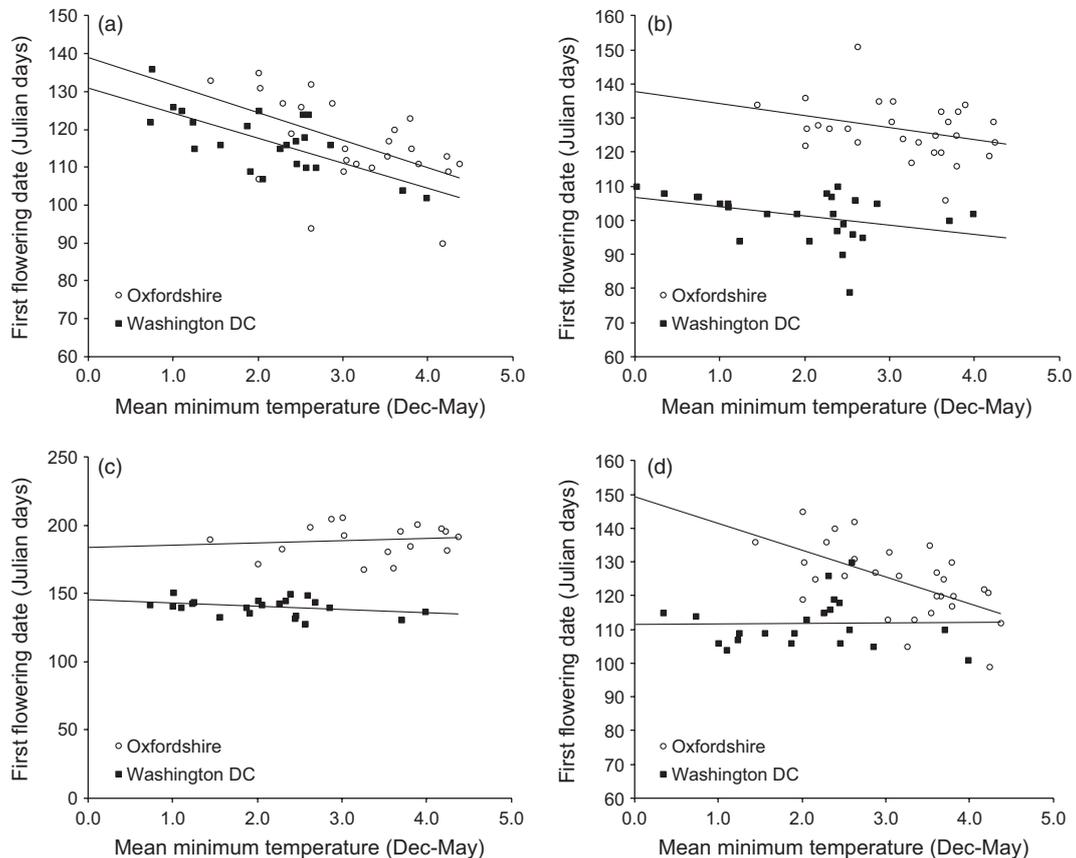


Fig. 2. Contrasting trait–environment relationships between the native (Oxfordshire, United Kingdom) and introduced (Washington, DC, USA) ranges described by the trend in first flowering date (FFD) and mean minimum temperature ($^{\circ}\text{C}$) between December and May. (a) *Plantago lanceolata* exhibiting similar relationships in both continents (equivalent to Fig. 1a); (b) *Barbarea vulgaris* which consistently flowered earlier in Washington, DC for the same mean temperature but exhibited the same rate of flowering advance in both ranges (equivalent to Fig. 1b); (c) *Cichorium intybus* also flowered earlier in Washington, DC for the same mean temperature but exhibited no relationship between FFD and temperature in either range (equivalent to Fig. 1c); and (d) *Chelidonium majus* revealed different FFD responses to temperature in each range (equivalent to Fig. 1d).

These phenological examples illustrate that trait–environment relationships facilitate the comparison of multiple species co-occurring within the same environmental niche space. The phenological patterns can be mapped onto the schematic representations in Fig. 1. Most species comparisons (12 of 19) exhibit significantly different mean trait (FFD) values but the slope of the relationship is similar in both regions, either positive (Fig. 1b) or non-significant (Fig. 1c). A smaller subset of species (4) show the same relationship in both regions with no difference in mean trait values (Fig. 1a), whereas another group of three species exhibit contrasting relationships with different slopes found in each continent (Fig. 1d). These examples provide insight into the performance of species in their native and introduced ranges that would not be obvious from a comparison of trait means or climate niches alone. The analysis also highlights that while differences may be found in trait–environment relationships, these may not necessarily be adaptive. Examination of trait–environment relationships cannot by themselves determine the degree to which differences are the result of genetic variation, phenotypic plasticity and/or genetic variation for phenotypic plasticity; such a distinction is best assessed through

subsequent common garden experiments. However, the trait–environment relationships provide a basis to develop more mechanistic hypotheses, pinpoint the traits of interest, ascertain the appropriate selection gradients (e.g. Colautti & Barrett 2010) and determine the range over which they need to be observed, as well as identify candidate species for further study.

As an example, at least two questions emerge from examination of the phenological trait–environment relationships in our data. First, is the generally consistent earlier flowering in Washington, DC simply a plastic response to the longer length of overwinter vernalisation? Such a test would require measuring FFD following experimental manipulations of winter temperatures on provenances from each continent for a subset of those species exhibiting the largest difference in mean FFD (Fig. 2b). Second, is the absence of temperature responsive FFD in Washington, DC adaptive? Similar experimental temperature manipulations would examine FFD in concert with a wider range of plant functional traits to enable fitness components to be estimated for different provenances of the three species that did not fit the otherwise consistent intercontinental trend (Fig. 2d).

Limitations of trait- and niche-based analyses of contemporary evolution in alien species

The limitations of trait- and niche-based approaches for investigating contemporary evolution in alien species may be circumvented by combining their differing perspectives to integrate knowledge of trait variation across the environmental space encompassed by species ranges. Quantifying how traits vary along environmental gradients in the native and introduced range is an essential first step in studies of contemporary evolution in biological invasions. Conducting these comparisons allows the formulation of testable hypotheses for common garden experiments and also places the outcomes from experiments into the wider context of range-wide species performance.

A wide range of possible trait–environment scenarios exist, which may reflect environmental matching, phenotypic plasticity and/or contemporary evolution (Fig. 1). Yet, our null expectation is that trait–environment relationships should be similar and driven by the same underlying processes in the native and introduced range. Thus, perhaps we should not be surprised when we find similar clinal variation in both the introduced and native range that reflects adaptation to the prevailing environment. Natural selection along environmental gradients has been shown to result in phenotypic differentiation and local adaptation among established alien plant populations (Colautti & Barrett 2010; Colautti, Eckert & Barrett 2010). Biological invasions provide opportunities to estimate how rapidly such local adaptation may occur in the introduced range. Given a long enough period since introduction and the possibility of multiple introductions, consistent patterns in trait variation between the native and introduced range are likely to be found along similar marked environmental gradients. However, to understand the success of invasive species, it is possibly of greater interest to distinguish when the character of adaptation differs between the introduced and native range. Thus, while clinal variation in traits of alien species is commonly found in the introduced range, the key question may not be whether this is due primarily to phenotypic plasticity and/or local adaptation but rather whether the relationship (and underlying mechanism) differs between the native and introduced range. For example, we might hypothesise that given the long residence time of species in their native range most trait variation along environmental gradients would be attributable to local adaptation with a lesser contribution arising from phenotypic plasticity, especially where dispersal among populations is limited (Sultan & Spencer 2002). In contrast, the comparatively short residence times and frequent long-distance movement of individuals as an alien plant species spreads in the introduced range may mean that pre-existing phenotypic plasticity plays a more prominent role than adaptation to local environments. Thus, it is those species that buck the trend of our null expectations that trait–environment relationships should be the same in the native and introduced range that might warrant further study to test hypotheses regarding the relative success or failure of alien species (Fig. 1d, e).

Evidence for local adaptation is normally tested using reciprocal transplants in common gardens in both the native and introduced range. While there are few alternatives to using this approach, common garden experiments are not always ideal for comparative assessments in some species, particularly those with long generation times, and results can often be quite specific to the location of the common garden (Williams, Auge & Maron 2008; Moloney *et al.* 2009). Given the logistical challenges of setting-up, maintaining and monitoring reciprocal common garden experiments for all but the most short-lived of plant species, an ability to target these experiments on key hypotheses would be valuable.

We suggest three ways where a better understanding of trait–environment relationships in the native and introduced ranges would result in improvements to the design of common garden studies. First, although many studies attempt to sample multiple populations across as wide an environmental gradient as possible in both the native and introduced range, such studies rarely quantify the trait variation of these source populations or relate it to dominant environmental gradients (Moloney *et al.* 2009). Such information would appear essential to inform what fitness components should be assessed in the common garden. Second, common gardens only sample a tiny proportion of the natural environmental gradients experienced by species, and it is important to know how local factors might influence trait variation. It would be necessary to know if common gardens sample a representative or biased sample of the environments that a species experiences under natural conditions. Third, the traits of species sampled from a wide latitudinal range are likely to be shaped by more than one environmental gradient (e.g. temperature, rainfall, photoperiod). Thus, understanding the relative magnitude of these gradients on trait variation would inform whether species in the native and introduced range experience similar gradients and provide expectations as to how traits might differ given the specific environmental conditions of the common garden(s). This would encourage common garden experiments to include manipulations of the local environment (e.g. irrigation, growing season length) that best encompass the main environmental gradients in each range. Including interesting and relevant environmental gradients compounds the difficulty of executing multiple common garden experiments, and as a result, examples of this type of research are infrequent (but see Alexander 2010).

Eco-evolutionary integration is particularly important to understand the interplay between alien species traits and recipient environments, but biologically realistic experimental assessments of the influence of evolution on ecological dynamics in the wild are relatively infrequent (Carroll 2011; Matthews *et al.* 2011), particularly studies that consider selection in the context of demographic, physiological and environmental factors. To date, these ecological, physiological and evolutionary perspectives on the success of alien species have largely been investigated independently, but it is clear that they all must be taken into account to understand the processes that shape biological invasions.

A range of tools needs to be integrated into future studies aimed at answering questions concerning contemporary

evolution in alien species. These include molecular genetic analyses to interpret introduction histories and source populations (Keller & Taylor 2008; Keller *et al.* 2009; Zhang, Zhang & Barrett 2010), studies of the pattern of quantitative genetic variation and covariation of ecologically relevant traits (Colautti & Barrett 2011), measurements of the intensity and type of natural selection acting on traits (Colautti & Barrett 2010) and reciprocal transplants among common gardens (Moloney *et al.* 2009). We propose that quantifying trait–environment relationships in both the introduced and native range is an under-valued but critical component of this set of integrated tools. The insights provided by the few studies that have compared trait–environment relationships in both the introduced and native range (Jakobs, Weber & Edwards 2004; Alexander *et al.* 2009; Hulme 2011a) highlight the utility of this approach in assessing the scope for contemporary evolution in biological invasions. Furthermore, there is increasing evidence that differences in climate niches on their own are insufficient to provide evidence for contemporary evolution. Therefore, there is a need to integrate species distribution models with a better understanding of underlying ecological and physiological processes (Kearney & Porter 2009; Morin & Thuiller 2009). We believe that comparative assessment of trait–environment relationships, followed-up by well-designed common garden experiments, will become of paramount importance in accurately predicting the future range shifts of invasive species.

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