

## Commentary

### Beware: alien invasion. Where to next for an understanding of weed ecology?

In this issue of *New Phytologist*, Dawson *et al.* (pp. 859–867) take an important step in assessing the role of plant traits, and plasticity therein, in determining invasiveness. They ask whether alien plant species that have *larger* invasion ranges also have *greater* plasticity in three functionally important traits: biomass, root/shoot ratio (*R:S*) and specific leaf area (SLA). This approach is novel in that it effectively treats invasiveness as a continuum, rather than a categorical (invasive/noninvasive) state. In addition it examines plasticity in ecologically significant plant functional traits, which is of interest given the association of these traits with global species distributions (see Wright *et al.*, 2004; Nicotra *et al.*, 2010).

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The ability of a species to respond to changes to environmental conditions, particularly increased resource availability, is often proposed to facilitate invasions (Baker, 1965; Davis *et al.*, 2000). 'Phenotypic plasticity' describes an organism's morphological, anatomical and developmental response to the environment (Schlichting, 1986). Analyses of the broad literature tend to support the concept that invasive plants display higher plasticity (Daehler, 2003; Davidson *et al.*, 2011; but see Palacio-López & Gianoli, 2011).

When asking a question about movement and potential diversification of species, the characteristics of species' lineages, and the shared evolutionary history of the species in these lineages, is important. Dawson *et al.* explicitly incorporate phylogeny into their meta-analysis and find differing degrees of phylogenetic structure in the traits they consider (little in biomass and SLA but quite a lot in *R:S* ratio). Overall their analyses shows that widespread invasive species have greater plasticity in biomass, but plasticity in both *R:S* and SLA is not correlated with number of regions invaded.

Dawson *et al.* conclude that focusing on the 'endpoint of trait plasticity' – the performance or fitness of the plant under different environmental conditions – may be a more fruitful approach than continued studies of plasticity in functional traits themselves. They recommend detailed field experiments on multiple co-occurring native and alien species. We agree that the endpoint of plasticity is critical, but as we discuss, we are reticent to discourage further consideration of plasticity in underlying functional traits.

#### When is plasticity important to the invasion process?

An invasion can be divided into two stages; (1) introduction and naturalization and (2) expansion of species (Williamson, 1996). Phenotypic plasticity may be involved directly in either or both stages. Dawson *et al.* analysed whether plasticity in functional traits is associated with stage two. It is possible that plasticity is more important for stage one, establishment in novel environments, than for spread or competitiveness (Palacio-López & Gianoli, 2011). Such a role for plasticity is consistent with suggestions that pioneer species may be more plastic than non-pioneer species (Bazzaz, 1979). Although invasive plants are generally pioneering species, in that they often establish in novel environments with very different climates from their home range (Gallagher *et al.*, 2010), not all pioneer plants are invasive. As such, there is a need for further investigation to separate whether plasticity is associated with pioneering characteristics and/or plays a more direct role in providing a competitive advantage of invasive species over the native flora.

With regard to stage two, it is likely that plasticity in functional traits would be related not simply to expansion of geographic range, but to increasing environmental range. This is a subtle but important difference. Dawson *et al.* assessed whether the number of regions invaded was correlated with levels of plasticity. This approach could be extended to address the more complicated issue of whether plasticity in functional traits is associated with the number of biomes/habitat types an invasive covers. The question then becomes one of how much larger an environmental range an invasive species can occupy and whether plasticity in functional traits facilitates this expansion.

It has also been proposed that instead of being a characteristic that increases the likelihood that a species will become invasive, plasticity may be a by-product of selection on changes to mean values of traits during invasion (rapid evolution of plasticity post-colonization; Agrawal, 2001). However, there is only limited support for the latter hypothesis: Colautti *et al.* (2009) found no consistent evidence of evolution for changes in mean trait values between native and invasive populations in a meta-analysis of 28 species. Likewise, glasshouse experiments paired with genetic analyses of invasive *Senecio inaequidens* plants

in Europe revealed the native population that was most closely related to the invasive populations also had the greatest phenotypic plasticity (Bossdorf *et al.*, 2008). Thus, it seems that high trait plasticity is a pre-existing characteristic of invasive species.

### Patterns of plasticity in functional traits may differ under stressful vs favourable conditions

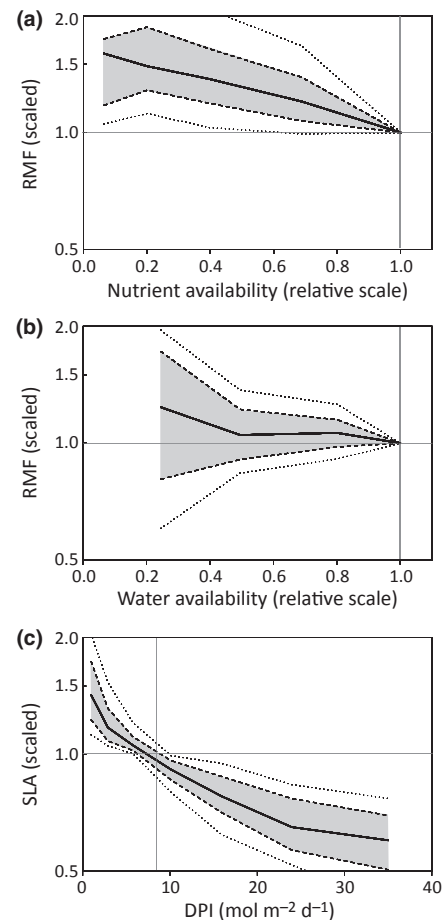
In evaluating the relative response of invasive and noninvasive species it is important to consider the environmental context. As described in Richards *et al.* (2006) and further discussed in Davidson *et al.* (2011) plasticity in underlying traits would be adaptive in an invasive species if it enabled a genotype to maximize fitness under optimal conditions ('master-of-some' response to increased resources) or maintain homeostatic fitness under poor conditions ('jack-of-all-trades' response to decreased resources) or both (jack-and-master). The master-of-some response provides a mechanism by which higher plasticity of invasive species could enable invasive species to out-compete native species and thus facilitate the invasion process.

Dawson *et al.* examined plasticity in response to an increase in resources; however, the range of conditions examined inevitably varied across studies within the meta-analyses. Especially in the context of climate change (e.g. increased frequency of drought events in many areas) it remains topical to differentiate between responses to a reduction in a resource below average conditions, and responses to an increase in that resource. For example, Davidson *et al.* (2011) found that, in response to a decrease in resources from average to deficient, native species were better able to maintain fitness homeostasis than co-occurring invasive species.

To put this in a slightly different context, Poorter *et al.* (2012) advocate the use of dose–response curves because measures of plasticity depend strongly on the conditions under which the plastic response (or reaction norm) is assessed. Rather than quantifying plasticity at a discrete interval (noting that Dawson *et al.* did include magnitude of resource level increase as a covariate for the chosen interval), a dose–response curve integrates over a wide range of conditions and investigates changes in the response across the conditions (Fig. 1; Poorter *et al.*, 2012). Thus, the question of whether invasive or noninvasive species differ in their ability to respond adaptively to *decreased* resource availability remains somewhat open.

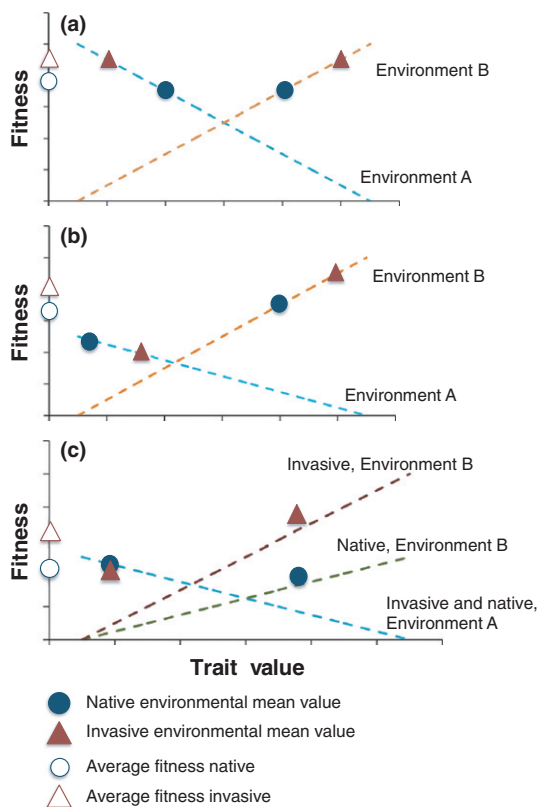
### The importance, and the challenge, of assessing relative performance

The adaptive value of a plastic response depends on whether it increases average net fitness (ideally taken as multigenerational fitness measures). Measuring fitness, however, is not a simple matter and relies on proxies, which must be selected with care (see Box 1 in Davidson *et al.*, 2011). Measurements of adaptive plasticity should also consider the representation of different conditions in the environment and assess the impacts of altering the frequencies/likelihoods of encountering these different resource conditions. Furthermore, one can consider adaptive plasticity at



**Fig. 1** Dose–response curves of the absolute response of the fraction of 10 whole plant mass represented by roots (RMF, analogous to the scaled root/shoot ratio (*R:S*) in Dawson *et al.*, this issue pp. 859–867) to (a) nutrient availability, (b) water availability and (c) of the response of specific leaf area (SLA) to light availability. Data are a compilation based on many species. For each environmental factor, a reference condition was chosen (indicated by a vertical line), and data for each species in each experiment were subtracted from the allocation values observed or interpolated for that reference level. The shaded area indicates the interquartile range (between 25th and 75th percentile) of the observed ratios in that part of the response curve. The dotted lines indicate the 10th and 90th percentiles. The bold continuous line within the shaded area indicates the median value. Both traits show plasticity, but in the case of the response of RMF to water availability in particular, the position of sampling points along the response curve will dramatically affect the estimate of plasticity. Figures modified with permission from <http://www.metaphenomics.org>; see Poorter *et al.* (2009, 2012) for further information.

different time scales: plasticity which was adaptive under past conditions and may be of neutral or maladaptive importance now; plasticity which is currently adaptive; and plasticity which may now be neutral or maladaptive but that could represent hidden adaptive potential under novel environments. Each of these is potentially important: the first for understanding the history of diversification of lineages, the second for understanding current selective pressures and the last for determining responses to future environments. The latter two are therefore relevant for understanding invasion biology and predicting responses to climate change.



**Fig. 2** Theoretical trait–fitness relationships across two environments (A and B) for a native/non-invasive and invasive species demonstrating three mechanisms (a–c) by which the invasive species may achieve greater average fitness than a native species. Closed symbols, mean trait values in each environment; open symbols, mean fitness for each species, across environments. (a) The invasive species displays greater plasticity than the native species (seen as a greater distance between the closed points) and higher average fitness. (b) The invasive displays higher average mean trait values than the native species which translates to higher average fitness despite identical levels of plasticity in both species. (c) The invasive displays a steeper relationship between the focal trait and fitness in environment B and therefore exhibits higher average fitness despite having the same mean trait values and plasticity as the native species.

In the context of invasions, however, the important question is not simply whether plasticity in a given trait is adaptive, but how the performance of invasive compared to native plants differs under the same conditions. Superior performance may be underpinned by greater plasticity, higher average mean trait values, steeper trait–fitness relationships or a combination of these (e.g. van Kleunen *et al.*, 2010; Godoy *et al.*, 2011; Fig. 2). For example, van Kleunen *et al.* (2010) found greater mean trait values for several functional traits in invasive compared to noninvasive species.

## Conclusions and future directions

We agree with Dawson *et al.*'s recommendations: to understand the role of plasticity in the spread of species (be it now, historically or in the future) will depend on detailed field experiments on multiple co-occurring native and alien species that include direct fitness measurements (including multigenerational fitness

where possible). Such multi-species studies, when conducted across a broad environmental range, also provide an ideal opportunity to examine under what circumstances plasticity in functional traits is important to fitness. So doing will enable us to examine the relationship between traits and their plasticity, and to identify when plasticity in one trait provides for homeostasis in another.

Understanding the role of plasticity and detecting patterns in adaptive plasticity of key functional traits and species types is important not only for managing invasions but also for managing populations under climate change (Sax *et al.*, 2007) and for improving modelling of species/community responses to climate change (Ghalambor *et al.*, 2007). Dawson *et al.* have shown that plasticity in biomass in response to increases in resources may be important for spread of invasive species, however many more questions remain. For example, what effect does position on the dosage response curve have? Does the response vary dramatically among species of different ecological, as well as evolutionary history? What effect does varying the likelihood of encountering different conditions have on the adaptive value of plasticity? Hypothesis driven meta-analyses, such as conducted by Dawson *et al.*, are useful to establish broad patterns regarding the likely role of plasticity in the invasion process or in responding to novel environments. These analyses provide a more informed starting point for essential empirical enquiries.

## Acknowledgements

The authors extend a big thanks to Hendrik Poorter for permission to use the figures from the <http://www.metaphenomics.org> website in this commentary.

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## References

- Agrawal AA. 2001. Phenotypic plasticity in the interactions and evolution of species. *Science* **294**: 321–326.
- Baker HG. 1965. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL, eds. *The genetics of colonizing species*. New York, NY, USA: Academic Press, 147–169.
- Bazzaz FA. 1979. The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**: 351–371.
- Bosdorf O, Lipowsky A, Prati D. 2008. Selection of preadapted populations allowed *Senecio inaequidens* to invade Central Europe. *Diversity and Distributions* **14**: 676–685.
- Colautti RI, Maron JL, Barrett SCH. 2009. Common garden comparisons of native and introduced plant populations: latitudinal clines can obscure evolutionary inferences. *Evolutionary Applications* **2**: 187–199.
- Daehler CC. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology Evolution and Systematics* **34**: 183–211.

- Davidson AM, Jennions M, Nicotra AB. 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 MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- Dawson W, Rohr RP, van Kleunen M, Fischer M. 2012. Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist* 194: 859–867.
- Gallagher RV, Beaumont LJ, Hughes L, Leishman MR. 2010. Evidence for climatic niche and biome shifts between native and novel ranges in plant species introduced to Australia. *Journal of Ecology* 98: 790–799.
- Ghalambor CK, Mckay JK, Carroll SP, Reznick DN. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology* 21: 394–407.
- Godoy O, Valladares F, Castro-Diez P. 2011. Multispecies comparison reveals that invasive and native plants differ in their traits but not in their plasticity. *Functional Ecology* 25: 1248–1259 (in English).
- van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245.
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F *et al.* 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.
- Palacio-López K, 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.
- Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Poorter H, Niklas KJ, Reich PB, Oleksyn J, Poot P, Mommer L. 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist* 193: 30–50.
- Richards CL, Bossdorf O, Muth NZ, Gurevitch J, Pigliucci M. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* 9: 981–993.
- Sax DF, Stachowicz JJ, Brown JH, Bruno JF, Dawson MN, Gaines SD, Grosberg RK, Hastings A, Holt RD, Mayfield MM *et al.* 2007. Ecological and evolutionary insights from species invasions. *Trends in Ecology and Evolution* 22: 465–471.
- Schlitching CD. 1986. The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics* 17: 667–693.
- Williamson M. 1996. *Biological invasions*. London, UK: Chapman and Hall.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

**Key words:** fitness, invasive, phenotypic plasticity, plant functional traits, weed.



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