It also is remarkable that qualitatively similar effects are induced in plants by a variety of plant-associated root-colonizing microbes, including plant growth-promoting rhizobacteria, *P. indica* and mycorrhizal fungi, as summarized in Shoresh *et al.* (2010). This is, apparently, an example of convergent evolution by very dissimilar organisms. Presumably, the ability of these microbes to induce changes in plants, resulting in a large number of healthy roots in which they live, provides a competitive advantage.

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**Trait divergence and the ecosystem impacts of invading species**

Invasions by exotic species pose significant threats to biological diversity, ecosystem functioning and human economies. Ecologists have long been fascinated by the mechanisms that allow an exotic species to establish in a new community (e.g. Elton, 1958) and there has been growing interest in connecting these mechanisms with the impacts of invasive species on ecosystem functioning (Levine *et al.*, 2003). In this issue of *New Phytologist*, a recent experiment by Scharfy *et al.* (pp. 818–828) compared abundant native and invasive species found in mesic herbaceous communities in northern Switzerland. They found that while invading species differed from native species in a few ways, they were remarkably similar to the native species in these communities. This same pattern could be predicted in many other plant communities based on a synthesis of theories regarding environmental influences on ecological strategies and community assembly.

‘... species origin is not a good predictor of competitive outcomes in communities ...’

Plant functional traits are often used as proxies to determine whether species have different ecological strategies for reproduction and resource capture (Lavorel & Garnier,
2002), and may provide mechanisms to explain which species are likely to invade, and which communities are likely to be invaded. Several theories predict that traits of invading species should be similar to traits of species in the native community. Plants growing in the same area are likely to share traits that are adaptive for the local climate because they have experienced similar environmental selection pressures (i.e. habitat filtering; Weih & Keddy, 1999). For example, species growing in infertile soils tend to have slow growth rates and increase their nutrient-use efficiency (NUE) by having thick, well-protected leaves with long leaf-longevity. Successful invaders in low-resource habitats are likely to also have these traits (Funk & Vitousek, 2007).

Neutral theory presents the null expectation that there should be few functional differences between native and invading species as long as there are similar suites of traits present in the pool of potential invaders (Daleo et al., 2009). By contrast, there are a variety of mechanisms that could lead to trait differences between native and invading species. The species pool of potential invaders is likely to be biased towards traits associated with long-distance dispersal or desirable qualities for humans, such as good forage quality. This hypothesis is supported by trait differences between native and invasive species found in analyses of regional and global species pools (Leishman et al., 2007; Ordonez et al., 2010; Van Kleunen et al., 2010). Similarly, niche-based community assembly theory predicts that successful invasive species should have different traits from native species; the concept of limiting similarity assumes that exotic species should use resources at different times or in different ways, otherwise they would be competitively excluded from the community (Abrams, 1983). Experiments with assembled communities have sometimes found that functionally distinct exotic species are more likely to successfully invade (Fargione et al., 2003; Hooper & Dukes, 2010; but see Emery, 2007). In addition to filling a vacant ecological niche, invading species may be able to establish because they are more plastic in response to resource pulses than are native species (Davis et al., 2000; Richards et al., 2006). In summary, these disparate theories produce a fundamental dichotomy in predictions regarding whether traits of invasive species should converge with species in the native community as a result of habitat filtering or neutral processes, or diverge as a result of limiting similarity, higher plasticity or biases in the introduced species pool (Grime, 2006).

Identifying patterns of trait divergence or convergence may also help to predict the potential impacts of invasion; Scharfy et al. hypothesized that invasive species would differ from native species in a suite of traits related to ecosystem impacts. To test this hypothesis they identified six common invasive forb species – three annuals and three perennials – and compared their traits with those of 12 dominant species from the native community – six perennial forbs and six perennial graminoids. Thus, there was an inherent starting bias in the study, in that there were so few invasive graminoids in these systems. They then screened these 18 species for 31 traits, including commonly measured leaf-level traits, whole-plant traits associated with resource uptake, plasticity in response to nutrient uptake and competition, traits related to soil impacts and allelopathic effect. To accomplish this trait screening they grew the focal species in a series of pot experiments, and measured a subset of traits in the field. Scharfy et al. found that the invasive forbs species tended to be very similar to the native forbs, differing only in having lower chlorophyll content. However, the forbs and the graminoids varied in a number of traits, such that the invasive forbs differed from the native graminoids by having a suite of traits such as shorter-lived leaves with lower tissue density and a lower NUE. As a consequence, the foliar tissues of the invasive forbs tended to decompose more quickly than those of the native graminoids, although not as fast as those of the native forbs. These trait differences led the authors to conclude that invasive forbs will alter ecosystem functioning if they invade areas dominated by native graminoids, but will not alter ecosystem functioning in areas dominated by native forbs, as a result of the trait similarity among forbs overall.

The comparative responses of the native vs invasive species to nutrient fertilization and competition were among the most surprising results in the study. A meta-analysis of native–invasive comparisons concluded that environmental context plays an important role in determining the relative performance of native and invasive species, and that native species frequently out-perform invasives when resources are limiting (Daehler, 2003). It has nearly become dogma that invasive species benefit more from resource enrichment than native species, but Scharfy et al. did not find this to be the case. Plasticity was measured in response to nutrient fertilization or competition with Holcus lanatus, a common and strongly competitive native grass in areas of northern Europe and a problematic invasive species in North America and Australia. They found that the focal native and invasive species showed similar increases in growth with fertilization, and although the full suite of native and invasive species were not grown in competition with one another, the invasive species tended to have a greater growth decline when grown in competition with a dominant grass than did the native species. Thus, the results of this study did not support the paradigm that successful invaders are better at pre-empting resource pulses, contributing to a higher competitive ability. Rather, these results suggest that species origin is not a good predictor of competitive outcomes in communities, and native species may frequently benefit from resource pulses if they have traits associated with high rates of growth and resource uptake (Maron & Marler, 2007).

Allelopathy is another mechanism that has been hypothesized to contribute to invasion. Scharfy et al. used Dactylis
glomerata as a phytometer to assess the allelopathic effects of the focal species, by growing D. glomerata in soil in which each focal species had been grown alone. The allelopathic effect was calculated as the percentage decrease in D. glomerata growth in the pre-grown soil to which activated charcoal had or had not been added, and plants had been fertilized. They found that invasive forbs had higher allelopathic effects than native forbs, but were similar to native graminoids. Thus, the pattern for allelopathic effects was at odds with the other trait differences, which tended to be greatest between forbs and graminoids, with few differences between the native and invasive forbs. From a niche-based perspective, this functional difference provides an axis of differentiation by which invasive forbs could gain a foothold when invading systems dominated by native forbs that are functionally similar in many regards. These results should be interpreted with some caution, however, because the allelopathic effects were discerned through the use of activated charcoal. Activated carbon is extremely porous and can bind an array of complex compounds, removing them from the soil solution. Recent work has shown that the addition of activated carbon can stimulate microbial activity and increase soil phosphate availability (Weißhuhn & Prati, 2009), suggesting that the positive effects of the addition of activated carbon may not be related to the attenuation of allelopathic effects, but rather could reflect functional differences in the way that these species interact with the soil microbial community.

Conclusions and future directions

Past efforts to identify trait differences between native and invasive species did not necessarily focus on ecosystem-level impacts; for instance, possession of small seeds may increase the likelihood of long-distance dispersal but does not have any a priori predicted effect on nutrient cycling rates (Lavorel & Garnier, 2002). Each species can be characterized by a large number of functional traits. Functional traits are frequently correlated with one another, such that suites of traits can be used to represent ecological strategies. For this reason, studies frequently employ multivariate clustering techniques to group species according to similar suites of traits, or collapse the multivariate trait data onto fewer axes that represent suites of correlated traits (e.g. Diaz et al., 2004). These multivariate techniques can identify trait-axes that represent the greatest trait convergence among species (traits associated with habit filtering), and trait-axes that identify where traits of native and invasive species diverge (traits related to potential ecosystem impacts). If the findings of Scharfy et al. hold in naturally assembled communities and other ecosystem types, we might expect to find one multivariate axis associated with habitat filtering where invading and native species within a community are similar, and an orthogonal axis representing potential differences among native and exotic species that predict ecosystem-level impacts (Fig. 1).

As global changes, such as invasion and climate change, increasingly impact natural systems, a ‘Holy Grail’ of plant ecology has become to predict how communities are likely to respond, and feed back, to influence ecosystem-level processes (Lavorel & Garnier, 2002; Suding et al., 2008). We may be able to predict ecosystem-level impacts of invasion if invading species differ from native species in traits that influence ecosystem properties, such as biogeochemical cycling, disturbance regime, energy balance or palatability to herbivores. Moving forward, we need a better understanding of whether the traits relating to establishment are correlated with increased abundance of invading species. Ultimately, invading species that become abundant and displace native species have the greatest potential to impact ecosystem function.

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Effect of segregation and genetic exchange on arbuscular mycorrhizal fungi in colonization of roots

Introduction

Arbuscular mycorrhizal fungi (AMF) are abundant soil organisms and form symbioses with roots of the majority of terrestrial plants (Smith & Read, 2008). The symbiosis with AMF can promote plant productivity and diversity, and tolerance to pathogens and to herbivores (Newsham et al., 1995; van der Heijden et al., 1998; Bennett et al., 2006; Bennett & Bever, 2007). The hyphae produced by spores are coenocytic, harbouring many nuclei in a common cytoplasm. Moreover, genetic differences among co-occurring nuclei have been observed and this explains the high intra-individual genetic diversity found in AMF (Pringle et al., 2000; Clapp et al., 2001; Kuhn et al., 2001; Rodriguez et al., 2004; Hijri & Sanders, 2005). Two processes related to the within-individual genetic variation in AMF have been recently demonstrated in the species Glomus intraradices and can affect the nucleotype content of an AMF in a very short time span (Croll et al., 2009; Angelard et al., 2010). First, genetic exchange between two genetically different AMF lines can lead to new spores having a mixture of parental nucleotypes (Croll et al., 2009). Second, one mother spore can produce new spores with different nucleotype contents as a result of the segregation of nucleotypes at spore formation (Angelard et al., 2010).