

INVITED REVIEW: PART OF A HIGHLIGHT ON TRAITS WITH ECOLOGICAL FUNCTIONS

A functional trait perspective on plant invasion

Rebecca E. Drenovsky^{1,†,*}, Brenda J. Grewell^{2,†,‡}, Carla M. D'Antonio³, Jennifer L. Funk⁴, Jeremy J. James^{5,‡}, Nicole Molinari³, Ingrid M. Parker⁶ and Christina L. Richards⁷

¹Biology Department, John Carroll University, University Heights, OH 44118-4581, USA, ²USDA-Agricultural Research Service Exotic & Invasive Weeds Research Unit, Department of Plant Sciences MS-4, University of California, Davis, CA 95616, USA, ³Environmental Studies Program, 4312L Bren, University of California, Santa Barbara, CA 93106, USA, ⁴School of Earth and Environmental Science, Chapman University, Orange, CA 92866, USA, ⁵USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center 67826-A Hwy 205, Burns, OR 97720, USA, ⁶Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA and ⁷Department of Integrative Biology, University of South Florida, Tampa, FL 33620, USA

[†]These authors contributed equally to this paper.

[‡]USDA is an equal opportunity provider and employer.

* For correspondence. E-mail rdrenovsky@jcu.edu

Received: 9 January 2012 Returned for revision: 20 February 2012 Accepted: 26 March 2012 Published electronically: 14 May 2012

- **Background and Aims** Global environmental change will affect non-native plant invasions, with profound potential impacts on native plant populations, communities and ecosystems. In this context, we review plant functional traits, particularly those that drive invader abundance (invasiveness) and impacts, as well as the integration of these traits across multiple ecological scales, and as a basis for restoration and management.
- **Scope** We review the concepts and terminology surrounding functional traits and how functional traits influence processes at the individual level. We explore how phenotypic plasticity may lead to rapid evolution of novel traits facilitating invasiveness in changing environments and then 'scale up' to evaluate the relative importance of demographic traits and their links to invasion rates. We then suggest a functional trait framework for assessing per capita effects and, ultimately, impacts of invasive plants on plant communities and ecosystems. Lastly, we focus on the role of functional trait-based approaches in invasive species management and restoration in the context of rapid, global environmental change.
- **Conclusions** To understand how the abundance and impacts of invasive plants will respond to rapid environmental changes it is essential to link trait-based responses of invaders to changes in community and ecosystem properties. To do so requires a comprehensive effort that considers dynamic environmental controls and a targeted approach to understand key functional traits driving both invader abundance and impacts. If we are to predict future invasions, manage those at hand and use restoration technology to mitigate invasive species impacts, future research must focus on functional traits that promote invasiveness and invader impacts under changing conditions, and integrate major factors driving invasions from individual to ecosystem levels.

Key words: Climate change, non-native plant, plant invasion, functional traits, plant traits, invasiveness, invader impacts.

INTRODUCTION

The synergistic effects of global environmental change and continued spread of non-native species present tremendous challenges for understanding and predicting how natural ecosystems will be altered over coming decades. Such an understanding is essential if we are to mitigate the negative effects of environmental change through ecological restoration. With the aim of improving human response to invasive species through both policy and management, three fundamental research needs are to (a) develop means to identify potentially harmful invasive plants; (b) assess the impacts of currently invasive plants to develop and prioritize management plans; and (c) develop invasive plant management and ecological restoration strategies in the context of changing environments. As a step towards these goals, we promote a plant trait-based approach for predicting invasion success and impact.

Many managers and scientists use the term 'invasive' to describe species that are introduced, establish, spread and eventually 'cause harm' (Mack *et al.*, 2000). Indeed, 'invasive' has been defined by the federal government in Executive Order 13112 to be non-native species that 'cause harm' to the environments that they invade. Generalizing the term in this way obscures the distinction between the process of invasion versus the process of developing impact and introduces the ill-defined concept of 'harm'. For the purposes of this paper, therefore, the term 'invasive' will only apply to plant species that establish and show or have potential for rapid spread in areas of introduction, rather than a more broadly applied definition that implies both abundance and negative impact. Ehrenfeld (2010) provides an extensive review of evidence that suggests many invasive plant species with measurable ecological impacts express traits that enhance their performance relative to native species and that simultaneously

result in alterations to ecosystem-level processes such as nutrient cycling. However, some attempts to identify traits associated with both invasion and impact have yielded mixed results or have not detected differences between invasive and native species (Daehler, 2003; Leishman *et al.*, 2010, Tecco *et al.*, 2010). This discrepancy underscores the complexity in predicting plant invasiveness and species impacts and the need for a framework for trait comparison (Ehrenfeld, 2010).

Significant progress has been made towards developing a general, conceptual framework for invasions, and more inclusive and mechanistic approaches to improve hypothesis testing of causal factors should lead to better understanding and management of biological invasions (Gurevitch *et al.*, 2011). In this review, we address the potential importance of plant functional traits across scales of ecological organization, across phases of invasion and impact, and within a restoration and management context. We first address the historical context and terminology associated with plant traits and environmental change. We then discuss functional traits at the level of the individual, delineating between different types of functional traits and assessment of their relative impacts on species performance and species effects in a system. Interpreting the role of functional traits naturally leads into a discussion of how plasticity in these traits may lead to rapid evolution and invader success in changing environments. ‘Scaling up’ to population-level processes, we review modelling tools used to evaluate the relative importance of individual traits, demographic rates and their links to invasion rates. We then discuss the difficulties in defining invader impacts on communities and ecosystems and suggest a functional trait framework for assessing per capita effects as well as traits affecting population growth that together may help predict ecological impact. In addition to assessing these effects, we suggest functional trait-based approaches in invasive species management and restoration in the context of environmental change.

PLANT FUNCTIONAL TRAITS: RESPONSE TO IMPACTS AT MULTIPLE SCALES

Much of the inspiration that led Darwin (1859) and Wallace (1870) to develop the theory of evolution came from their biogeographical observations of how trait variation influences survival and fitness. Elton’s seminal work highlighting concerns over invasive, non-native species suggested that invasive species have unique traits that allow them to exploit species-poor communities (Elton, 1958). He predicted the most successful non-native species would have traits that promote effective reproduction and dispersal, superior competitive ability, and the ability to occupy vacant niches (Elton, 1958). Since Elton’s work, there has been intense interest in understanding what makes a plant species ‘invasive’. Baker (1965) identified a suite of plant traits that an ‘ideal weed’ might possess, and postulated that weedy plant species have combinations of advantageous traits that could explain variation in invasiveness. He did not address species impacts *per se*. Growing awareness of non-native plant invasions and their potential impacts prompted new efforts to identify plant traits of widely abundant invaders (e.g. Rejmánek and Richardson, 1996; Reichard and Hamilton, 1997;

Rejmánek, 2000; Grotkopp *et al.*, 2002; Rejmánek *et al.*, 2005a; Richardson and Pyšek, 2006; Herron *et al.*, 2007). This research was driven by a desire to understand controls over invasion success and improve risk assessment and habitat management. However, it did not specifically recognize the difference between traits affecting invasiveness versus those affecting impact.

Recently, the term ‘functional trait’ has been broadly applied to analyses of species traits, and the meaning of the term has varied when applied across scales of ecological organization. Some researchers propose that the use of the term be restricted to attributes of individual plants without reference to the environment or other levels of ecological organization (Violle *et al.*, 2007). Because we are specifically interested in characterizing response to novel and changing environments, for our purposes, functional plant traits are the readily measurable morphological, chemical, physiological and phenological attributes of plants that interact with surrounding biotic and abiotic factors. Thus, within bounds, their expression is expected to change with the environment. Given this context, we use the phrase ‘functional trait framework’ to describe conceptual linkages among functional traits and biological, ecological and evolutionary processes involved in the invasion of non-native plants.

Functional traits have been viewed and defined in various ways. Some studies have emphasized that variation in individual plant traits can take the form of a continuous range rather than discrete classes (Chapin *et al.*, 1996). ‘Discrete’ plant traits are typically qualitative individual traits that are strongly related to phylogeny (e.g. eudicot/monocot, N-fixer/not), while ‘continuous’ traits [e.g. specific leaf area (SLA), leaf life span, seed size, photosynthetic capacity] are attributes that all species have and can be quantified on a continuum even if varying widely among species (Chapin *et al.*, 1996; Reich *et al.*, 2003). Other works have differentiated plant functional traits based on their ease of measurement. ‘Hard’ plant traits are those that directly influence plant function yet are difficult or time-consuming to measure in experimental time [e.g. dispersal distance, relative growth rate (RGR), competitive effect and response], whereas ‘soft traits’ are more readily quantifiable (Weiher *et al.*, 1999). Perhaps the most commonly reported soft trait is leaf mass per unit area (LMA) or its inverse, SLA, which correlates with RGR (Lambers and Poorter, 1992), photosynthetic rate (Wright *et al.*, 2004), leaf nitrogen (N) content (Reich *et al.*, 1997) and leaf lifespan (Westoby *et al.*, 2002), and is thought to be the most useful single indicator of leaf strategy (i.e. the ecological trade-off between resource capture and resource conservation). However, given the diversity of taxa and life forms that have become invasive, as well as the variety of ecosystems that have been invaded, expecting one trait to be a universal predictor of invasive potential is unrealistic (Grotkopp *et al.*, 2010). Additionally, soft traits may not be suitable analogues for hard traits at the community level or in restoration practice (Grotkopp *et al.*, 2010; Kooyman *et al.*, 2010; Leishman *et al.*, 2010). Multiple, mechanistic pathways link soft and hard traits, and some relationships may be more or less important in different species or environmental conditions. For example, both physiological and morphological traits influence RGR,

which will be high in a rapidly growing and spreading invader. Although the soft trait SLA is often a strong predictor of RGR in invasive species (e.g. Grotkopp and Rejmánek, 2007; James and Drenovsky, 2007), for some species, the physiological component, net assimilation rate is a stronger predictor of RGR (Grotkopp *et al.*, 2010). Additionally, traits that are advantageous in resource-rich environments (e.g. less dense, poorly defended tissues) may be disadvantageous for plants invading resource-poor environments where slow growth and tissue retention are important (Berendse, 1994).

Recognition of the link between functional traits and processes across multiple ecological scales (e.g. fitness, community assembly, ecosystem function) has prompted a surge of research to improve trait-based approaches (e.g. Lavorel and Garnier, 2002; Violle *et al.*, 2007). Early attempts to predict large-scale plant community responses to global environmental change were based on how individual plants responded to environmental factors, and plant traits were integrated as key filters in community assembly models (Woodward and Cramer, 1991; Keddy, 1992; Woodward and Diament, 1996). Suites or syndromes of plant traits (e.g. slow tissue turnover, low transpiration rates, high root mass ratio, high concentrations of secondary metabolites) also were correlated with responses to variation in limiting resources (Chapin *et al.*, 1993). Several contributions then turned the focus more specifically to multiple plant ‘effect traits’, which can alter community and ecosystem responses to environmental change (Chapin *et al.*, 2000; Chapin, 2003; Mack and D’Antonio, 2003; Eviner and Chapin, 2003). Many ‘effect’ traits (Díaz and Cabido, 2001) correspond with ecosystem processes such as primary productivity, nutrient cycling and trophic transfer. For example, LMA, leaf N content, and leaf area ratio affect primary productivity while phenology and litter quality affect nutrient cycling rates (Funk *et al.*, 2008). Some traits may be both ‘response’ and ‘effect’ traits. For example, low LMA may reflect the ability of a plant to respond rapidly to enhanced resource availability while also creating particular effects on primary productivity and nutrient cycling. The trait-based effects on ecosystem-level processes have been sufficiently documented to be incorporated into global models (Chapin, 2003; Díaz *et al.*, 2004) and have supported a move to frameworks which link response and effect traits with species interactions to predict global-change impacts (e.g. Lavorel and Garnier, 2002; Suding *et al.*, 2008).

Based on this body of previous work we recognize the importance of differentiating effect traits from response traits (i.e. traits that are considered to only respond to the abiotic or biotic environment) at multiple scales of invasion and ecological organization. We accept a broad definition of plant functional trait to include any attribute that responds to biotic or abiotic factors (such as resource availability, disturbance or herbivore pressure) as well as traits that influence ecosystem processes (such as primary productivity, nutrient cycling and trophic transfer). Although some authors consider functional traits only at an individual plant level, we argue that some plant traits are measurable properties that can be scaled to populations, communities or ecosystems (e.g. Vile *et al.*, 2006; Shipley, 2010). Therefore, our definition encapsulates all of these levels, and provides a broad perspective for

understanding how non-native plant species respond to and influence the ecosystems they invade.

FLEXIBLE TRAITS: THE ROLE OF PHENOTYPIC PLASTICITY

Phenotypic plasticity is the ability of a particular genotype to express a range of phenotypes across different environments (Bradshaw, 1965), which may be adaptive (Dudley and Schmitt, 1996; van Kleunen and Fischer, 2005; Richards *et al.*, 2006). The plasticity of key functional traits may be particularly beneficial during the invasion process and to all plants facing a changing climate (Baker, 1965; Richards *et al.*, 2006; Nicotra *et al.*, 2010). Typically, during the invasion process only a few individuals or even one genotype are responsible for establishing a population. Theory predicts that the genetic bottleneck caused by this colonization process limits a species’ phenotypic options and therefore the potential for evolution by natural selection.

Despite these expected limitations, many invasive species succeed in novel locations with low levels of genetic variation (Hollingsworth and Bailey, 2000; Dlugosch and Parker, 2008a, b; Richards *et al.*, 2008; Loomis and Fishman, 2009; Zhang *et al.*, 2010). In a review of 80 introduced plant, animal and fungal species, the average loss of molecular-level diversity from the native range to the introduced range was found to be substantial (Dlugosch and Parker, 2008a). However, most ecologically important traits are quantitative traits under the control of many genes and, in contrast to the molecular studies, Dlugosch and Parker found only one published study that reported a substantial decline in quantitative trait variation in the new range (Simberloff *et al.*, 2000). This suggests that decreased genotypic variation in introduced populations may not necessarily translate into reduced phenotypic variation. One limitation is that few studies have compared variation in quantitative traits between the native and introduced range (Dlugosch and Parker, 2008a). Given the central importance of functional and life-history traits in shaping invasion success and impact, we argue that this is a major gap in our understanding of how traits and their variation will influence invasions.

Due to the low level of genotypic diversity in many invading species, several authors have suggested that phenotypic plasticity could be an important source of the phenotypic variation seen in introduced populations. Phenotypic plasticity enhances niche breadth (Bradshaw, 1965; Van Valen, 1965; Donohue *et al.*, 2001; Sultan, 2001; Richards *et al.*, 2005), and therefore it logically follows that plasticity may enable invaders to succeed under novel conditions without large amounts of DNA sequence-based diversity. In a recent meta-analysis of 75 phylogenetically related species pairs, plant species classified as ‘invasive’ were more plastic in a wide variety of morphological and physiological traits than native, non-invasive species (Davidson *et al.*, 2011). This greater plasticity could indicate either that (a) inherently more plastic species are more likely to be successful invaders or (b) that plastic genotypes within species were selected during the invasion process (Donohue *et al.*, 2001; Etterson, 2004; Yeh and Price, 2004; Kaufman and Smouse, 2001;

Sexton *et al.*, 2002; Parker *et al.*, 2003). Carefully designed comparative studies are required to tease apart these different scenarios, which may vary with species and environment (Richards *et al.*, 2006; van Kleunen *et al.*, 2010a).

As with any other trait, in order for phenotypic plasticity to be important in invasions, it must be related to fitness (Richards *et al.*, 2006). Three theoretical frameworks have been proposed for phenotypically plastic invasive species (Baker, 1965; Richards *et al.*, 2006). In the first case, invaders maintain high fitness across a wide range of environments due to morphological and physiological plasticity, akin to the 'general purpose genotype' (Baker, 1965) or fitness homeostasis (Hoffman and Parsons, 1991; Rejmánek, 2000). In the second case, compared with other resident plant species, the most successful invaders are better able to take advantage of, and have greater increase in, fitness in favourable environments, due to morphological and physiological plasticity, while persisting under less than optimal conditions (Sultan, 2001). Further, the third case would be an 'ideal weed' (*sensu* Baker, 1965), which would combine these two strategies and be able to maintain fitness across a broad range of environments but also be able to opportunistically take advantage of favourable environments by increasing fitness. In the context of environmental change, predicting and understanding the plasticity of invasive species under these different scenarios has important implications for management and restoration. If many individuals of the invading population are able to maintain high fitness, invader abundance and therefore impact should increase. However, if invasive species are only able to maintain high fitness under specific environmental conditions, their impacts may be more spatially or temporally limited.

While these predictions make intuitive sense, a recent meta-analysis of 45 native/invasive species pairs demonstrated convincingly that while invaders expressed higher plasticity, they did not have higher fitness in response to increased resources (Davidson *et al.*, 2011). When resources were limited, the invasive species were also more plastic but the natives maintained greater fitness in 16 species pairs. Thus, these data suggest that increased phenotypic plasticity may not always translate into greater fitness and therefore may not always account for invasive species success. While phenotypic plasticity of key invader traits may be observed and quantified, our knowledge of its role in the invasion process under field conditions is limited (Hulme, 2008). In particular, there is a need for improved understanding of plasticity's role in dispersal, colonization, persistence and abundance (Hulme, 2008), especially as it relates to our ability to predict how species and communities will respond to changing environmental conditions (Suding *et al.*, 2008). Because of phenotypic plasticity, levels of phenotypic variation within-species can be as large as between species (Jung *et al.*, 2010). There may also be species-specific limits to plasticity; e.g. modelling studies suggest that some plants have limited capacity to alter leaf stomatal conductance in response to rising atmospheric CO₂ (de Boer *et al.*, 2011). Therefore, the complexities of understanding phenotypic plasticity can complicate scaling up species-level processes to higher levels of ecological organization (Nicotra *et al.*, 2010). These knowledge gaps surrounding the plasticity of functional traits can complicate assessment

of plant species impacts on communities and ecosystems, particularly from a management perspective.

While the contribution of plasticity to the invasion process is not well understood, studies have shown that plasticity is genetically based and therefore can evolve like other traits. More recently, several authors have argued that in addition to DNA sequence-based differences in phenotype and phenotypic plasticity, epigenetic effects (i.e. DNA methylation, histone modification, small interfering RNA) also can contribute to ecologically important phenotypic differences (Rapp and Wendell, 2005; Richards, 2008; Bossdorf *et al.*, 2008, 2010; Johannes *et al.*, 2009; Jablonka and Raz, 2009; Richards *et al.*, 2010a, b). Epigenetic effects can be especially active in response to hybridization and exposure to stressful or novel environments (Rapp and Wendel, 2005; Salmon *et al.*, 2005; Chinnusamy and Zhu, 2009; Verhoeven *et al.*, 2010), which are circumstances often experienced by invasive plants. Because epigenetic changes can be elicited by environmental factors and are stably inherited, they supply a potentially rapid mechanism for the inheritance of plastic responses (Bossdorf *et al.*, 2008; Richards *et al.*, 2010a, b). Richards *et al.* (2008) provide evidence for this possibility in *Fallopia japonica* populations that have invaded a diversity of habitats with high levels of phenotypic variation that persists in common garden. Across populations, they found almost no sequence variation, but using methylation-sensitive AFLP (amplified fragment length polymorphism), Richards and colleagues showed that these populations harbour five times as many polymorphic epigenetic loci as DNA sequence loci (C. L. Richards *et al.*, unpubl. res.). Bottleneck effects combined with epigenetic effects can lead to divergent phenotypes in invasive populations even in the absence of abundant sequence-based variation (Keller and Taylor, 2008; Prentis *et al.*, 2008). Thus, there is a need for invasion studies specifically designed to tease apart the various components of phenotypic variance, which will, in turn, enhance our general understanding of adaptation processes.

EVALUATING PLANT TRAITS: THE DEMOGRAPHIC PERSPECTIVE

While the average response and plasticity of functional traits are clearly important for the success of individuals within a population, they also contribute directly to the demographic rates that ultimately determine population persistence or failure in changing environments. Detailed demographic analysis incorporates the relationship between particular traits or life history attributes and plant fitness, and goes a step further to link plant performance to population abundance. Invasive species have specific combinations of traits that allow them to succeed through dispersal, colonization and expansion phases of the invasion process and, in some cases, to competitively displace resident species in the novel environment. By linking functional traits (e.g. lifespan, fecundity) with the tools of population modelling, we have a quantitative way to assess the ecological importance of different traits from a demographic perspective.

Population models integrate demographic rates across the life cycle, providing information on the growth rates and dynamics of populations (Caswell, 2001). Density-independent

models, such as most matrix population models, have been used to explore population growth rates of invasive plants and how they respond to environmental variation (e.g. Shea and Kelly, 1998; Parker, 2000; Jacquemyn *et al.*, 2005; Koop and Horvitz, 2005; Hyatt and Araki, 2006; Sebert-Cuvillier *et al.*, 2007; Engelen and Santos, 2009; Griffith, 2010). Density-dependent models, in which the number of plants recruiting into the population is limited by an environmental carrying capacity, are needed for any investigations that focus not on rates of spread, but on the final abundance reached by an invader (Sheppard *et al.*, 2002; Buckley *et al.*, 2004), which may be strongly tied to the impacts of the invader (i.e. at lower abundance, impacts may be less severe). Lastly, matrix population models that are spatially explicit (Neubert and Caswell, 2000) can be used to integrate data on functional traits related to dispersal with demographic traits to investigate how each of these sources of variation can influence invasion (Neubert and Parker, 2004; Buckley *et al.*, 2005; Jongejans *et al.*, 2008).

Of the many demographic analyses, perturbation analysis (elasticity and sensitivity analyses) readily lends itself to making the link between functional traits and population growth, abundance or spatial spread in the context of environmental change. Perturbation analysis indicates how population growth responds to small changes in each of the transitions throughout the life cycle (i.e. the relative importance of each transition to population growth). Perturbation analysis has been used effectively to address management questions for invasive plants. Ideally, perturbation analysis can be used to search for an ‘Achilles’ heel’ of the invader (*sensu* Parker, 2000): if population growth rate is highly sensitive to one demographic transition or vital rate, that life stage could be the target of management efforts. Although a single vulnerable life stage is rarely found, population models have been very useful tools for assessing the potential or realized effectiveness of management, especially the introduction of biological control agents (e.g. Shea and Kelly, 1998; Paynter, 2005; Davis *et al.*, 2006; DeWalt, 2006; Schutzenhofer and Knight, 2007; Paynter *et al.*, 2010). These approaches can provide insight into how ecological complexity, such as variation in time and space in environmental conditions or biotic interactions, can influence the relative importance of different parts of the life cycle (e.g. Shea *et al.*, 2005; DeWalt, 2006). For example, Prevey *et al.* (2010) found that the relative contribution of annual and biennial life histories to population growth in *Tragopogon dubius* changed in response to rain manipulations.

In the same way, these modelling approaches can provide insight into the relative importance of different functional traits or of the same trait expressed at different times of the life cycle. For example, a demographic model might reveal that population growth is much more sensitive to seedling growth rate than it is to adult growth rate. In this case, RGR at the seedling stage would be a more important functional trait than RGR at the adult phase. A study of the same species under conditions of climate warming might show that seed survival during dormancy and, therefore, seed defence traits, suddenly becomes the most important factor influencing population growth under projected future conditions.

In addition to the ‘prospective’ perturbation analyses we have just discussed, one may also break down observed

patterns of variation in population growth, calculating the relative importance of different life stage transitions to these patterns, using ‘retrospective’ perturbation analysis such as life table response experiments (LTRE) (Caswell, 2000). This tool allows us to evaluate the population-level consequences of observed differences in functional traits among sites, years or management approaches. For example, the shrub *Cytisus scoparius* invaded native prairie sites more rapidly than disturbed urban fields (Parker, 2000). While many life-cycle transitions were substantially different between the two habitats, LTRE analysis revealed that early establishment was by far the most important factor driving observed differences in invasion rates of *C. scoparius*. This information could inform future studies on functional traits most likely to influence the early establishment stage, such as germination behaviour or drought tolerance of seedlings. Thus, by linking demography to environmental conditions, a more targeted approach to functional trait studies can be pursued.

While a lengthy discussion of caveats is not within the scope of this review, we will mention that traditional sensitivity analysis as applied to matrix population models (as well as LTRE analysis) assumes a stable stage distribution (i.e. the relative proportions of individuals in different life stages stay the same and produce the same overall rate of population growth from year to year). In fact, however, a newly invading population may not usually be at the stable stage distribution. Therefore, analyses of transient dynamics may be important for invasive plants and may sometimes provide a quantitatively different view from traditional sensitivity analyses (McMahon and Metcalf, 2008).

UNTANGLING TRAITS ASSOCIATED WITH ECOLOGICAL IMPACTS

Demographic processes, and traits there associated, link to invasion rates and plant abundance, which ultimately influence plant impacts at community and ecosystem scales. Risk assessment protocols are typically used to categorize invasive plants according to their potential impacts (Randall *et al.*, 2008). Traits leading specifically to impacts should thus be a key part of risk assessment modelling. For example, in California, only 132 of the >1800 naturalized plant species are considered to have measurable community and ecosystem impacts in wildland settings (www.cal-ipc.org) and only 38 of these are listed as having ‘severe’ or ‘high’ impacts. The traits defining these different groups of non-native plants have not been comprehensively assessed. An understanding of which traits lead to the different types and levels of impact is at the heart of prioritizing invasive species for control and management.

Over the past three decades, several reviews of invasive plant impacts have been conducted, spanning the range from population to ecosystem impacts (e.g. D’Antonio and Vitousek, 1992; Daehler and Strong, 1993; Ehrenfeld, 2003, 2006, 2010; Levine *et al.*, 2003; Vilá *et al.*, 2011). Yet, compared with our understanding of which traits allow a species to become invasive, our understanding of traits related to species impacts is fragmentary (Levine *et al.*, 2003; Rejmanek *et al.*, 2005b) and case specific, such as the well-studied case of species effects on N accumulation and cycling (e.g. Vitousek *et al.*, 1987; D’Antonio and Corbin, 2003; Ehrenfeld, 2003;

Hughes and Denslow, 2005). This is in part because most studies that evaluate traits of invaders compared with resident or native species or non-invasive congeners focus on traits that affect invasiveness and not impact *per se* (e.g. van Kleunen *et al.*, 2010b). A challenge to devising a framework for predicting plant impact traits lies in the concept and definition of ‘impact’ itself, as there is no one definition or agreement on level at which the effects of an individual or group of individuals becomes an impact of concern. A single plant can have multiple effects on the environment immediately around it. These effects are due to both the capture of resources by the individual and the presence and activity of the individual itself. For example, individual plants deplete nutrients immediately in their rooting zone but also enhance nutrient availability by exuding carbon, which promotes microbial breakdown of soil organic matter outside of the root. These effects are not necessarily measurable at a scale that is important to plant community dynamics: they are per capita effects of the individual, but they do not by themselves create an impact. At the scale that managers care about, plant impact is a function of both per capita effects from the traits that cause them and the cumulative abundance of individuals of that species in the environment, particularly relative to other species. This conceptualization of impact was proposed by Parker *et al.* (1999) when they suggested that a universal definition of a species impact was $I = A \times R \times E$, where A = abundance, R = range and E = per capita effects. In this equation both A and R are representative of abundance but at different scales (local versus regional or national), and they reflect an interaction of demographic plant traits with the environment. In terms of response or effect traits, species traits associated with A and R are most likely response traits. E or per capita effects, on the other hand, represents morphological, physiological and chemical interactions of the plant and its attributes with its environment and most likely represent E traits that directly affect the environment and indirectly influence fitness.

Critical to this discussion is the distinction between ‘invasiveness’ and ‘impacts’. There are many naturalized species that once introduced, have spread quite broadly, yet they have very little measurable impact (Richardson *et al.*, 2000). These are typically not well studied because of their lack of impact, but examples might include widespread forbs in North America such as *Senecio vulgaris*, *Stellaria media* or *Erodium* species that can be locally abundant but do not appear on noxious or wildland weed lists, or *Cakile edentula*, a fast-spreading non-native plant that became widespread quickly but is not very competitive (Boyd and Barbour, 1993). Although these species have traits that promote high population growth and spread (demographic traits), their per capita effects are low. Conversely, some species may have a limited ability to spread across the environment but they have large effects on their immediate environment. For example, *Eucalyptus globulus* in California does not spread rapidly, yet each individual plant deposits large amounts of chemically rich litter, thus potentially creating a large local impact on the understorey environment (personal observation of the authors, and see Sax, 2002). This species is on the ‘moderate impacts’ list of the California Invasive Plant Council’s list because of the recognition of its generally slow spread. Thus, the Parker *et al.* (1999) framework is useful in clarifying

the difference between an ‘effect’ and an ‘impact’ and between traits associated with abundance and ‘invasiveness’ versus those associated with per capita effects. Additionally, this framework demonstrates that invasiveness is important to impact severity because it is related to local and regional abundance. However, invasiveness is not equivalent to impact. This has been recognized recently for animal species as well: in a review, Ricciardi and Cohen (2007) found little relationship between ‘invasiveness’ and ‘impacts’ for a range of vertebrates. Likewise, invasiveness is not the same as local and regional abundance, which has more to do with carrying capacity than with spread. A species might be slow-growing and slow spreading, but within a 200-year time frame (without active control/management) could fill the same space as a species with a much higher population growth rate. Ultimately the one with a bigger carrying capacity will have the bigger impact, all E traits being equal.

Similarly, controls over population growth of an invader are not the same as controls over its impacts. For example, *Carpobrotus edulis*, a succulent, mat-forming perennial plant introduced to California from South Africa, spreads most rapidly in dune and back-dune habitats in California (D’Antonio, 1993; Molinari *et al.*, 2007). Its spread into adjacent coastal shrublands is slow due to intense and persistent herbivory by native vertebrate herbivores (D’Antonio, 1993). Nonetheless, on a per individual basis, its per capita effects (E) are higher in the shrublands than in the dunes (D’Antonio, 1990; Molinari *et al.*, 2007). In the former, it reduces soil pH, overgrows and diminishes native species (D’Antonio and Mahall, 1991) and creates much more litter accumulation at the soil surface (Molinari *et al.*, 2007). Its per capita effects in the nearby back dune are much less remarkable and native species there appear better at coexisting with it than they are in the shrubland. This example highlights the context dependency of E traits and overall impact for a single invader species as well as the ways in which traits affecting population growth and spread interact with E traits to create impact.

An additional challenge to developing a framework for predicting impact is that there are many different types of measured or purported impacts, so a wide range of traits should be expected to create impact. These impacts can vary in magnitude and duration and may arise through indirect effects of traits, so there is no simple metric for comparing them. One example, yellow star thistle, *Centaurea solstitialis*, has been purported to reduce rangeland productivity, reduce deep soil water storage (Gerlach, 2004; Enloe *et al.*, 2004) and reduce native species diversity (www.cal-ipc.org). The latter impact has not been substantiated but is nonetheless cited as a prime concern to land managers. These three impacts span from economic impacts (productivity of rangeland for livestock production), to impacts on an ecosystem process and resource pool (water), to community-scale effects (biodiversity). While such distinctions may be disappearing at the management scale as ecosystem services become monetized (e.g. Kobayashi *et al.*, 2010), mechanistically from a trait perspective they are distinct: each impact presumably arises because of a different suite of plant traits. Spines (a morphological trait), for example, make the plant unpalatable, thereby reducing forage quality, while a deep taproot (unrelated to

spines), can access water below the rooting zone of co-occurring grasses and more shallowly rooted forbs, thus reducing deep soil-water storage.

Likewise, impacts of concern such as fire risk in arid and semi-arid ecosystems (e.g. D'Antonio and Vitousek, 1992) can arise through multiple different trait pathways. For example, in Hawaiian dry forests, traits associated with drought tolerance and shallow soil summer water uptake have allowed invasive African grasses to reduce the productivity of native forest species thus indirectly increasing fire risk and threatening the loss of native species (Cordell and Sandquist, 2008). In the Great Basin (western USA), the ability of the annual grass *Bromus tectorum* to germinate abundantly in wet years and create a continuous fuel bed directly increases ignition probability and thus fire risk (e.g. Whisenant, 1990). While the common functional trait here is plant fuel class (abundant 'fine fuel'), the means through which the impact (fire) is created relies on different hard trait combinations and pathways.

The pathways through which the impacts of plant invaders on biodiversity arise are generally poorly understood, despite this being an important concern of managers. Although there are examples of species-specific or site-specific ties between functional traits and reduced native species diversity, such as when ignitable non-native grasses described above reduce native diversity by fueling destructive wildfires (e.g. Whisenant, 1990; Hughes *et al.*, 1991), generalized patterns across invader taxa and systems remain elusive. This is true even within a single functional group of invaders. For example, invasive N fixers have traits (e.g. high seed production and persistent seed banks, rapid growth via N-fixation) that promote high population abundance as well as having large impacts on nutrient cycling (e.g. Vitousek *et al.*, 1987; Vitousek and Walker, 1989). These traits may be linked to the suppression of native vegetation via rapid growth and shading or direct facilitation of other fast-growing invaders (e.g. Hughes and Denslow, 2005), but cross-site and cross continental research highlights the variability of these impacts and the need for a thorough understanding of multiple traits that interplay to drive both invasion and impact (Stock *et al.*, 1995; Yelenik *et al.*, 2007; Le Maitre *et al.*, 2011; Morris *et al.*, 2011).

Traits related to one clearly defined type of impact are easier to identify than trait syndromes that lead to multiple consequences in the invaded environment. However, from an applied perspective, those traits and their associated impacts that are easy to identify may not be the same as those that are of management concern. Invaders that affect N cycling, for example, are presumed to enhance it through the creation of low carbon-cost leaves that decompose readily (e.g. Vitousek and Walker, 1989; Baruch and Goldstein, 1999; Ehrenfeld, 2003; Allison and Vitousek, 2004; Liao *et al.*, 2008). Yet, for many managers nutrient cycling is not the impact of concern, particularly if the invader is not associated with increased N pool sizes (such as with N-fixing invaders). If the impact of concern is 'reductions in native species', then we need to identify a mechanistic link (e.g. Cordell and Sandquist, 2008). For N cycling, we must understand how rapidly decomposing leaves may lead to growth inhibition of native species. Traits associated with more rapid decomposition (e.g. low lignin : N and C : N ratios) are typically associated with fast growth and low LMA. Yet, these traits may not be associated

with long-term persistence and hence long-term impacts, unless the initial high N cycling invader creates a strong positive feedback or promotes other invaders that in turn replace or keep out native species (e.g. Hughes and Denslow, 2005). Such positive feedbacks have been hypothesized about for decades, but their existence and importance are poorly demonstrated in the field (Ehrenfeld *et al.*, 2005). Thus, the direct impacts of a fast-growing, high leaf N invader (that is not an N fixer) may in reality be short lived, while long-term impacts will depend on whether other undesirable species are enhanced by the original invader or whether natives can return to the site as the initially fast-growing species declines.

The key points are that (a) impacts for any given species arise due to a combination of traits that reflect per capita effects and that influence invader abundance, and (b) the trait syndromes of importance will depend on the type of impact evaluated as well as the time frame. Thus, a framework for predicting impacts based on plant traits will be most robust when specific impacts are identified, mechanistic links can be elucidated and compared, and when an understanding of time-scale is included. Traits that lead to reduced native biodiversity will prove to be more complex because there are both direct and indirect pathways through which invaders create such impacts. Trait syndromes leading eventually to altered biodiversity are thus likely to be system specific and as yet have not been comprehensively addressed.

MANAGEMENT AND RESTORATION OF INVADED PLANT COMMUNITIES IN CHANGING ENVIRONMENTS

We advocate a functional trait framework for restoring plant communities, as functional traits are critical for predicting invasive-species spread and impact under different environmental change scenarios and also form the basis for identifying effective strategies for restoring invaded systems. Additionally, functional traits of invaders and trait distribution within native plant communities influence invasiveness and invasion resistance and therefore are central drivers of invasive plant abundance (Mouillot *et al.*, 2007; Scharfy *et al.*, 2011). As outlined in the previous section, both abundance and per capita effects of species on their environments influence invasive plant impact. Thus, prediction and management of invasion under future climate-change scenarios, as well as restoration of invaded systems, requires an understanding of functional traits that determine invader abundance and spread and how functional traits drive differences in per capita effects of species on their environment. In this section we outline how functional traits influence invasion resistance and invasive plant impacts. We also identify key knowledge gaps and discuss limitations and the potential of using functional traits to improve restoration and invasive plant management outcomes.

The influence of plant functional traits on invasion resistance has been a central question in community ecology with immediate practical links to invasive species management (Pokorný *et al.*, 2005). Initially, this line of work focused on the influence of species and functional group diversity on invasion resistance. Quantitative synthesis of this research has suggested that species and functional group diversity may be poor

predictors of invasion resistance (Wright *et al.*, 2006). Alternatively, hypotheses based on limiting trait similarity (MacArthur and Levins, 1967) predict that species with functional traits most similar to the invader will play the largest role in invasion resistance. In addition, the mass ratio hypothesis proposed by Grime (1998) predicts that ecosystem properties and processes are not only driven by functional effect traits of individual species but also by how species abundance is distributed in the community. Thus, differences in effect traits among species may not necessarily translate into differences in how species affect ecosystem properties, such as invasion resistance. For example, James *et al.* (2008) showed that subdominant species differed from dominant species in their timing and depth of soil N acquisition. They also found that subdominant species had patterns of N acquisition that were comparable to the invasive species, suggesting subordinate species would play a significant role in invasion resistance. However, when they weighted species N acquisition by species abundance in the plant community, dominant species were the main sink for N, regardless of soil depth or time, and also were the only species that significantly contributed to invasion resistance.

Thus, to maximize invasion resistance, practitioners need to consider the functional effect traits of native species relative to the invader, the diversity of effect traits that can be managed, as well as species abundance. The first choice for managers would be to establish and maintain dominant species that have functional effect traits (e.g. rooting depth, SLA) comparable to invaders (Pokorny *et al.*, 2005). From a practical perspective, however, the success and impact of many invaders may be because they differ significantly from the dominant species in effect traits (e.g. N fixation, phenology, life history). In these likely more common scenarios, where no-analogue environments support novel plant community assemblages, managers may not constrain species selection to the historically dominant native species pool but may instead select non-native species that will recover critical ecological functions and inhibit invader spread. In these scenarios, managers must balance strategies and practices that maximize invasion resistance but that may compromise other objectives, such as increasing and maintaining biodiversity (Boyd and Svejcar, 2009). Thus, while a functional trait approach may have practical limitations and constraints, it provides a predictive framework for understanding how management decisions influence changes in plant functional traits, and thus invasive species spread and impact.

Functional traits also may suggest ways that abiotic factors (e.g. environmental filters) within a restored system can be manipulated to favour native plants at the expense of non-native invaders. Work in a disturbed montane rainforest in Hawaii suggested that the success of light reductions to understorey seedlings could be predicted based on a few key leaf-level traits (LMA, chlorophyll content, light-use efficiency) (Funk and McDaniel, 2010). These traits could be used to identify heliophilic invaders as well as shade-tolerant native species for planting in restored, closed canopies. In another study, the effectiveness of soil N reductions on reducing invasive species growth in a desert annual community were linked to leaf N status and the timing of germination (Steers *et al.*, 2011). In normal precipitation years, invasive species germinated

weeks before native species and were strongly affected by low soil N availability, resulting from carbon added to the soil during the first rain event of the season. However, when the system received several early-season storms, native and invasive species germinated simultaneously, and both experienced reduced growth in response to soil N depletion.

Despite these promising results, there are several significant knowledge gaps that limit our ability to fully implement a functional trait framework for invasive plant management. One central challenge to management, and an area of much needed research, is to understand and predict when and how per capita effects increase but invasive plant abundance remains the same or decreases. For example, in many situations per capita effects increase as abundance increases or per capita effects decrease as abundance decreases (Chambers *et al.*, 2007). However, there are also situations in which per capita effects increase while abundance decreases (D'Antonio, 1990; Molinari *et al.*, 2007).

Second, most of our understanding of functional trait differences between native and invasive species comes from established plants and plant communities. For example, a common question in community assembly research has focused on the role of SLA (inverse of LMA) in structuring communities, with the idea that high-SLA (low LMA) species will be distributed in more resource-rich or less stressful portions of the gradient compared with low-SLA species (Jung *et al.*, 2010). Traits correlated with differences in assembly, however, are not necessarily traits that cause differences in assembly. Processes occurring early on, such as dispersal and establishment are known to play a central role in community assembly (Grubb, 1977), yet we know comparatively little about how variations in these functional traits impact community assembly and, therefore, plant response to environmental change. For example, a recent study in shrub steppe systems showed that the primary driver of species recruitment and abundance following disturbance was centred on traits that influenced the probability that germinated seeds emerged (James *et al.*, 2011). Once seedlings emerged, abundance changed little. Thus, traits of juvenile and adult plants such as SLA and the degree to which these traits determine impact can play a smaller role than traits that directly influenced demography and recruitment.

Third, knowing which combinations of traits and environmental factors result in establishment and spread of a continuum of native to non-native species is relevant to understanding plant community assembly and invasion biology (Davis, 2009). Recognizing how functional trait variation interacts with community assembly processes may be key to effective invasive plant management and ecological restoration. Resource conservation traits may place established native plants at a competitive advantage over invasive plants in resource-poor systems. However, when both native and invasive species recruit from the seed bank, greater propagule pressure, early germination, greater seedling survivorship, and/or faster seedling growth by invasive species compared with native species may provide invaders an initial advantage in resource-poor and resource-rich systems; as a result, a long-term barrier to native plant recruitment, regardless of initial habitat conditions, may occur (Von Holle and Simberloff, 2005; DiVittorio *et al.*, 2007;

Abraham *et al.*, 2009; James *et al.*, 2011). Because many plant traits influence assembly processes, management of environmental filters may not result in the community response predicted by resource-use traits alone.

Functional trait data can serve as a valuable basis for decision making by practitioners and allow prediction of how plant communities and land management activities will influence restoration outcomes and invasion resistance. The prediction of the path that plant communities will follow in alternative restoration scenarios is a major challenge, but decision making by practitioners can be improved by adopting a scientific approach that includes ecological principles that are often overlooked in the restoration process (Zedler, 2000). The concepts outlined in this paper that use functional traits to assess per capita effects and impacts of invasive and native plants make a major advancement towards improved predictability and decision making. Many new trait databases are being compiled (e.g. Kattge *et al.*, 2011), which will facilitate trait-based approaches to restoration. Land managers have already employed this type of information to make practical changes to policy and procedures and to improve restoration outcomes. For example, in the arid western United States, managers have seeded over 250 000 ha a year in efforts to rehabilitate land damaged by catastrophic fire. Historically, there has been vigorous debate on whether to seed these landscapes with introduced species that have a high probability of establishing and preventing spread of invasive species or seeding landscapes with native species that have a low probability of establishing and preventing spread of invasive species. Functional trait data have been very useful in developing a compromise in this debate and, consequently, improving management policy decision making. Namely, scientists have identified functional traits characteristic of introduced plant species with high rates of establishment and then used this information to select and grow native accessions that contain these key traits, resulting in higher native plant seeding success and improved control of invasive species spread (Jones and Monaco, 2007; Rowe and Leger, 2011). Overall, the functional trait framework developed in this paper can improve management decision making because it links concepts of functional trait variation, plasticity and demography to advance understanding and prediction of invasive plant impacts. Continued development of this approach and assessment of how traits yield impact across multiple-scales is critical as environmental change forces managers to deal with shifts in species ranges and plant assembly in novel ecosystems.

CONCLUDING REMARKS

Ultimately, our goal is to understand the factors driving abundance and impacts of invasive species not only under current conditions, but also in response to environmental change. To do so, we must be able to link trait-based changes in response to fluctuating environments to changes in community and ecosystem properties. In order to scale up from organismal-level traits, research must move beyond the consideration of how single species or traits are influenced by changing environmental conditions; instead, changes in abundance and impacts must be summed across the community as a whole (Suding

et al., 2008). Additionally, few trait-based studies of invasive species include more than two levels of a given abiotic factor (Richards *et al.*, 2006), limiting their predictive power. Therefore, a comprehensive effort must be grounded in a firm understanding of demographic processes that influence abundance (Gurevitch *et al.*, 2011), a targeted approach to identify key functional traits that influence our impacts of interest (Suding *et al.*, 2008), and inclusion of multiple levels of environmental drivers (Richards *et al.*, 2006), particularly under field conditions (Hulme, 2008).

To date, most studies have focused on a subset of major phenomena that define invasions (i.e. rapid population increase, establishment of local dominance or monocultures, rapid range expansion, and/or major ecosystem alteration; Gurevitch *et al.*, 2011), despite early calls for more integrated approaches (Vitousek, 1990; Schierenbeck *et al.*, 1994). Additionally, most conceptual frameworks for biological invasions currently are based on limited supporting evidence, and many are focused solely on population interactions or community ecology, excluding the consideration of processes occurring at multiple ecological scales (Gurevitch *et al.*, 2011). These frameworks, although they help us understand invasiveness (e.g. van Kleunen *et al.*, 2010b), do not directly address the impacts of invasive species. From a restoration and management perspective, both aspects are key to predicting future invasions, managing current invasions and mitigating species impacts.

We know that plant functional traits influence and impact key ecosystem processes (Ehrenfeld, 2010). However, our knowledge of how functional traits scale across levels of ecological organization or spatial and temporal scales is still limited (Messier *et al.*, 2010), and site-specific relationships may limit our ability to generalize trait–impact relationships. Moreover, some species (e.g. ecosystem engineers at high abundance) may have disproportionate effects on communities and ecosystems (Vitousek, 1990; Jones *et al.*, 1994). Given these caveats, large databases compiling functional trait data across species and biomes (e.g. Kattge *et al.*, 2011) provide an unprecedented opportunity to investigate questions from a global perspective and may help disentangle site-specific effects from global paradigms. Additionally, preliminary work suggests that community assembly is critically linked to traits, rather than species units *per se*, due to environmental filters selecting for traits conveying success in a given environment (Messier *et al.*, 2010). Lastly, the problem of disproportionate impacts stresses the importance of understanding abundance (i.e. invasiveness) and impacts together.

Anthropogenic-driven environmental change further complicates prediction and management of plant invasions. However, by explicitly measuring demographic traits, targeting specific impacts and their related functional traits, incorporating developing paradigms from large-scale datasets and meta-analyses, and specifically designing experiments that allow for multiple environmental change outcomes will improve our knowledge of the functional traits of invasive species that (a) promote invasiveness, and (b) convey impacts across multiple levels of biological and ecological organization. In turn, this research should improve our ability to identify and manage invasive species better, as well as design proper restoration scenarios.

ACKNOWLEDGEMENTS

We thank T. Rost and two anonymous reviewers for suggestions that improved our manuscript. We acknowledge the Ecological Section of the Botanical Society of America for supporting the symposium that brought us together.

LITERATURE CITED

- Abraham JK, Corbin JD, D'Antonio CM. 2009. California native and exotic perennial grasses differ in their response to soil nitrogen, exotic annual grass density, and order of emergence. *Plant Ecology* **201**: 445–456.
- Allison SD, Vitousek PM. 2004. Rapid nutrient cycling in leaf litter from invasive species in Hawai'i. *Oecologia* **141**: 612–619.
- Baker HG. 1965. Characteristics and modes of origin of weeds. In: Baker HG, Stebbins GL. eds. *The genetics of colonizing species*. New York, NY: Academic Press, 147–168.
- Baruch Z, Goldstein G. 1999. Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawai'i. *Oecologia* **121**: 183–192.
- Berendse F. 1994. Competition between plant populations at low and high nutrient supplies. *Oikos* **71**: 253–260.
- de Boer HJ, Lammertsma EI, Wagner-Cremer F, Dilcher DL, Wassen MJ, Dekker SC. 2011. Climate forcing due to optimization of maximal leaf conductance in subtropical vegetation under rising CO₂. *Proceeding of the National Academy of Sciences of the USA* **108**: 4041–4046.
- Bosdorf O, Richards CL, Pigliucci M. 2008. Epigenetics for ecologists. *Ecology Letters* **11**: 106–115.
- Bosdorf O, Arcurri D, Richards CL, Pigliucci M. 2010. Experimental alteration of DNA methylation affects the phenotypic plasticity of ecologically relevant traits in *Arabidopsis thaliana*. *Evolutionary Ecology* **24**: 541–553.
- Boyd CS, Svejcar TJ. 2009. Managing complex problems in rangeland ecosystems. *Rangeland Ecology & Management* **62**: 491–499.
- Boyd R, Barbour MJ. 1993. Replacement of *Cakile edentula* by *C. maritima* in the strand habitat of California. *American Midland Naturalist* **130**: 209–228.
- Bradshaw AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**: 115–155.
- Buckley YM, Rees M, Paynter Q, Lonsdale M. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia. *Journal of Applied Ecology* **41**: 547–560.
- Buckley YM, Brockerhoff E, Langer L, Ledgard N, North H, Rees M. 2005. Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology* **42**: 1020–1030.
- Caswell H. 2000. Prospective and retrospective perturbation analyses: their roles in conservation biology. *Ecology* **81**: 619–627.
- Caswell H. 2001. *Matrix population models: construction, analysis, and interpretation*, 2nd edn. Sunderland, MA: Sinauer Associates.
- Chambers JC, Meyer SE, Whittaker A, Roundy BA, Blank RR. 2007. What makes Great Basin sagebrush ecosystems invulnerable to *Bromus tectorum*? *Ecological Monographs* **77**: 117–145.
- Chapin FSIII. 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Annals of Botany* **91**: 455–463.
- Chapin FSIII, Autumn K, Pugnaire F. 1993. Evolution of suites of traits in response to environmental stress. *American Naturalist* **142**: S78–S92.
- Chapin FS, Reynolds H, D'Antonio CM, Eckhart V. 1996. The functional role of species in terrestrial ecosystems. In: Walker B, Steffen W. eds. *Global change in terrestrial ecosystems*. Cambridge: Cambridge University Press, 403–428.
- Chapin FSIII, Zavaleta ES, Eviner VT, et al. 2000. Consequences of changing biotic diversity. *Nature* **405**: 234–242.
- Chinnusamy V, Zhu JK. 2009. Epigenetic regulation of stress responses in plants. *Current Opinion in Plant Biology* **12**: 133–139.
- Cordell S, Sandquist DR. 2008. The impact of an invasive African bunchgrass (*Pennisetum setaceum*) on water availability and productivity of canopy trees within a tropical dry forest in Hawaii. *Functional Ecology* **22**: 1008–1017.
- Davis MA. 2009. *Invasion biology* Oxford: Oxford University Press.
- 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.
- Daehler CC, Strong DR. 1993. Prediction and biological invasions. *Trends in Ecology and Evolution* **8**: 380–381.
- D'Antonio CM. 1990. Seed production and dispersal in the non-native, invasive succulent *Carpobrotus edulis* in coastal strand communities of central California. *Journal of Applied Ecology* **27**: 693–702.
- D'Antonio CM. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent, *Carpobrotus edulis*. *Ecology* **74**: 83–95.
- D'Antonio CM, Corbin JD. 2003. Effects of plant invaders on nutrient cycling: using models to explore the link between invasion and development of species effects. In: Canham CD, Cole JJ, Lauenroth WK. eds. *Models in ecosystem science*. Princeton, NJ: Princeton University Press, 363–384.
- D'Antonio CM, Mahall BE. 1991. Root profiles and competition between the invasive, exotic perennial, *Carpobrotus edulis*, and two native shrub species in California coastal scrub. *American Journal of Botany* **78**: 885–894.
- D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass-fire cycle and global change. *Annual Review of Ecology and Systematics* **23**: 63–88.
- Darwin C. 1859. *On the origin of species*. London: John Murray.
- Davis AS, Landis DA, Nuzzo V, Blossey B, Gerber E, Hinz HL. 2006. Demographic models inform selection of biocontrol agents for garlic mustard (*Alliaria petiolata*). *Ecological Applications* **16**: 2399–2410.
- 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.
- DeWalt SJ. 2006. Population dynamics and potential for biological control of an exotic invasive shrub in Hawaiian rainforests. *Biological Invasions* **8**: 1145–1158.
- Díaz S, Cabido M. 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution* **16**: 646–655.
- Díaz S, Hodgson JG, Thompson K, et al. 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science* **15**: 295–304.
- DiVittorio CT, Corbin JD, D'Antonio CM. 2007. Spatial and temporal patterns of seed dispersal: an important determinant of grassland invasion. *Ecological Applications* **17**: 311–316.
- Dlugosch KM, Parker IM. 2008a. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology* **17**: 431–449.
- Dlugosch KM, Parker IM. 2008b. Invading populations of an ornamental shrub show rapid life history evolution despite genetic bottlenecks. *Ecology Letters* **11**: 701–709.
- Donohue K, Pyle EH, Messiqua D, Heschel MS, Schmitt J. 2001. Adaptive divergence in plasticity in natural populations of *Impatiens capensis* and its consequences for performance in novel habitats. *Evolution* **55**: 692–702.
- Dudley SA, Schmitt J. 1996. Testing the adaptive plasticity hypothesis: density-dependent selection on manipulated stem length in *Impatiens capensis*. *American Naturalist* **147**: 445–465.
- Ehrenfeld JG. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* **6**: 503–523.
- Ehrenfeld JG. 2006. A potential novel source of information for screening and monitoring the impact of exotic plants on ecosystems. *Biological Invasions* **8**: 1511–1521.
- Ehrenfeld JG. 2010. Ecosystem consequences of biological invasions. *Annual Reviews of Ecology Evolution and Systematics* **41**: 59–80.
- Ehrenfeld JG, Ravit B, Elgersma K. 2005. Feedback in the plant-soil system. *Annual Reviews of Environment and Resources* **30**: 75–115.
- Elton CS. 1958. *The ecology of invasions by animals and plants*. London: Methuen.
- Engelen A, Santos R. 2009. Which demographic traits determine population growth in the invasive brown seaweed *Sargassum muticum*? *Journal of Ecology* **97**: 675–684.
- Enloe SF, DiTomaso JM, Orloff SB, Drake DJ. 2004. Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses. *Weed Science* **52**: 929–935.

- Etterson JR. 2004. Evolutionary potential of *Chamaecrista fasciculata* in relation to climate change. I. Clinal patterns of selection along an environmental gradient in the Great Plains. *Evolution* **54**: 1446–1458.
- Eviner VT, Chapin FSIII. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annual Review of Ecology, Evolution, and Systematics* **34**: 455–485.
- Funk JL, McDaniel S. 2010. Altering light availability to restore invaded forest: the predictive role of plant traits. *Restoration Ecology* **18**: 865–872.
- Funk JL, Cleland EE, Suding KN, Zavaleta. 2008. Restoration through re-assembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* **23**: 695–703.
- Gerlach JD Jr. 2004. The impacts of serial land-use changes and biological invasions on soil water resources in California, USA. *Journal of Arid Environments* **57**: 365–379.
- Griffith AB. 2010. Positive effects of native shrubs on *Bromus tectorum* demography. *Ecology* **91**: 141–154.
- Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* **86**: 902–910.
- Grotkopp E, 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.
- Grotkopp E, Rejmanek M, Rost T. 2002. Toward a causal explanation of plant invasiveness: seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* **159**: 396–419.
- Grotkopp E, Erskine-Ogden J, Rejmanek M. 2010. Assessing potential invasiveness of woody horticultural plant species using seedling growth rate traits. *Journal of Applied Ecology* **47**: 1320–1328.
- Grubb PJ. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews of the Cambridge Philosophical Society* **52**: 107–145.
- Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* **14**: 407–418.
- Herron PM, Martine CT, Latimer AM, Leicht-Young SA. 2007. Invasive plants and their ecological strategies: prediction and explanation of woody plant invasion in New England. *Diversity and Distributions* **13**: 633–644.
- Hoffman AA, Parsons PA. 1991. *Evolutionary genetics and environmental stress*. Oxford: Oxford University Press.
- Hollingsworth ML, Bailey JP. 2000. Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese knotweed). *Botanical Journal of the Linnean Society*, **133**: 463–472.
- Hughes RF, Denslow JS. 2005. Invasion by a N₂ fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecological Applications* **15**: 1615–1628.
- Hughes FR, Vitousek PM, Tunison JT. 1991. Alien grass invasion and fire in the submontane zone of Hawai'i. *Ecology* **72**: 743–746.
- Hulme PE. 2008. Phenotypic plasticity and plant invasions: is it all Jack? *Functional Ecology* **22**: 3–7.
- Hyatt LA, Araki S. 2006. Comparative population dynamics of an invading species in its native and novel ranges. *Biological Invasions* **8**: 261–275.
- Jablonka E, Raz G. 2009. Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *Quarterly Review of Biology* **84**: 132–176.
- Jacquemyn H, Brys R, Neubert MG. 2005. Fire increases invasive spread of *Molinia caerulea* mainly through changes in demographic parameters. *Ecological Applications* **15**: 2097–2108.
- James JJ, Drenovsky RE. 2007. A basis for relative growth rate differences between native and invasive forb seedlings. *Rangeland Ecology and Management* **60**: 395–400.
- James JJ, Davies KW, Sheley RL, Aanderud ZT. 2008. Linking nitrogen partitioning and species abundance to invasion resistance in the Great Basin. *Oecologia* **156**: 637–648.
- James JJ, Drenovsky RE, Monaco RM, Rinella MJ. 2011. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecological Applications* **21**: 490–502.
- Johannes F, Porcher E, Teixeira FK, et al. 2009. Assessing the impact of transgenerational epigenetic variation on complex traits. *PLoS Genetics* **5**: e1000530. <http://dx.doi.org/10.1371/journal.pgen.1000530>.
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* **69**: 373–386.
- Jones TA, Monaco TA. 2007. A restoration practitioner's guide to the restoration gene pool concept. *Ecological Restoration* **1**: 12–17.
- Jongejans E, Skarpaas O, Shea K. 2008. Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology Evolution and Systematics* **9**: 153–170.
- Jung V, Violle C, Mondy C, Hoffmann L, Muller S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology* **98**: 1134–1140.
- Kattge J, Díaz S, Lavorel S, et al. 2011. TRY – a global database of plant functional traits. *Global Change Biology* **17**: 2905–2935.
- Kaufmann SR, Smouse PE. 2001. Comparing indigenous and introduced populations of *Melaleuca quinquenervia* (Cav.) Blake: response of seedlings to water and pH levels. *Oecologia* **127**: 487–494.
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* **3**: 157–164.
- Keller SR, Taylor DR. 2008. History, chance and adaptation during biological invasion: separating stochastic phenotypic evolution from response to selection. *Ecology Letters* **11**: 852–866.
- van Kleunen M, Fischer M. 2005. Constraints on the evolution of phenotypic plasticity in plants. *New Phytologist* **166**: 49–60.
- van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M. 2010a. Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters* **13**: 947–958.
- van Kleunen M, Weber E, Fischer M. 2010b. A meta-analysis of trait differences between invasive and noninvasive plant species. *Ecology Letters* **13**: 235–245.
- Kobayashi M, Rollins K, Taylor MH. 2010. Ranching, invasive annual grasses, and the external costs of wildfire in the Great Basin: a stochastic dynamic programming approach. Selected Paper 11955, Agricultural and Applied Economics Association Series Paper 61869, 2010 Annual Meeting, Denver, Colorado, 25–27 July 2010, <http://purl.umn.edu/61869> (accessed 20 November, 2011).
- Koop AL, Horvitz CC. 2005. Projection matrix analysis of the demography of an invasive, nonnative shrub (*Ardisia elliptica*). *Ecology* **86**: 2661–2672.
- Kooyman R, Cornwell W, Westoby W. 2010. Plant functional traits in Australian subtropical rain forest: partitioning within-community from cross-landscape variation. *Journal of Ecology* **98**: 517–525.
- Lambers H, Poorter H. 1992. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**: 187–261.
- Lavorel S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* **16**: 545–556.
- Leishman MR, Thomson VP, Cooke J. 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. *Journal of Ecology* **98**: 28–42.
- Le Maitre DC, Gaertner M, Marchante E, et al. 2011. Impacts of invasive Australian acacias: implications for management and restoration. *Diversity and Distributions* **17**: 1015–1029.
- Levine JM, D'Antonio CM, Dukes JS, Grigulus K, Lavorel S, Vilá M. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society* **270**: 775–781.
- Liao CZ, Peng RH, Luo YQ, et al. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist* **177**: 706–714.
- Loomis ES, Fishman L. 2009. A continent-wide clone: population genetic variation of the invasive plant *Hieracium aurantiacum* (Orange Hawkweed; Asteraceae) in North America. *International Journal of Plant Sciences* **170**: 759–765.
- McMahon SM, Metcalf CJE. 2008. Transient sensitivities of non-indigenous shrub species indicate complicated invasion dynamics. *Biological Invasions* **10**: 833–846.
- MacArthur R, Levins R. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* **101**: 377–387.
- Mack RN, D'Antonio CM. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecological Applications* **13**: 154–166.
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences and control. *Ecological Applications* **10**: 689–710.

- Messier J, McGill BJ, Lechowicz MJ. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**: 838–848.
- Molinari N, D'Antonio CM, Thomson G. 2007. *Carpobrotus* as a case study of the complexities of species impacts. In: Cuddington K, Byers J, Hastings A, Wilson W. eds. *Ecosystem engineers: concepts, theory and application in ecology*. San Diego, CA: Academic Press, 139–162.
- Morris TL, Esler KJ, Barger NN, Jacobs SM, Cramer MD. 2011. Ecophysiological traits associated with the competitive ability of invasive Australian acacias. *Diversity and Distributions* **17**: 898–910.
- Mouillot D, Mason NWH, Wilson JB. 2007. Is the abundance of species determined by their functional traits? A new method with a test using plant communities. *Oecologia* **152**: 729–737.
- Neubert MG, Caswell H. 2000. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. *Ecology* **81**: 1613–1628.
- Neubert MG, Parker IM. 2004. Using integrodifference equations to project rates of spread for invasive species. *Risk Analysis* **24**: 817–831.
- Nicotra AB, Atkin OK, Bonser SP, et al. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**: 684–692.
- Parker IM. 2000. Invasion dynamics of *Cytisus scoparius*: a matrix model approach. *Ecological Applications* **10**: 726–743.
- Parker IM, Simberloff D, Lonsdale WM, et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**: 3–19.
- Parker IM, Rodriguez J, Loik ME. 2003. An evolutionary approach to understanding the biology of invasions: local adaptation and general-purpose genotypes in the weed *Verbascum thapsus*. *Conservation Biology* **17**: 59–72.
- Paynter Q. 2005. Evaluating the impact of a biological control agent *Carmentia mimosae* on the woody wetland weed *Mimosa pigra* in Australia. *Journal of Applied Ecology* **42**: 1054–1062.
- Paynter Q, Main A, Gourlay AH, Peterson PG, Fowler SV, Buckley YM. 2010. Disruption of an exotic mutualism can improve management of an invasive plant: varroa mite, honeybees and biological control of Scotch broom *Cytisus scoparius* in New Zealand. *Journal of Applied Ecology* **47**: 309–317.
- Pokorny ML, Sheley RL, Zabinski CA, Engel RE, Svejcar TJ, Borkowski JJ. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* **13**: 448–459.
- Prentis PJ, Wilson JR, Dormontt EE, Richardson DM, Lowe AJ. 2008. Adaptive evolution in invasive species. *Trends in Plant Science* **13**: 288–294.
- Prevey JS, Germino MJ, Huntly NJ. 2010. Loss of foundation species increases population growth of exotic forbs in sagebrush steppe. *Ecological Applications* **20**: 1890–1902.
- Randall JM, Morse LE, Benton N, Hiebert R, Lu S, Killeffer T. 2008. The invasive species assessment protocol: a tool for creating regional and national lists of invasive non-native plants that negatively impact biodiversity. *Invasive Plant Science and Management* **1**: 36–49.
- Rapp RA, Wendel JF. 2005. Epigenetics and plant evolution. *New Phytologist* **168**: 81–91.
- Reich PB, Walters MB, Ellsworth DS. 1997. From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA* **94**: 13730–13734.
- Reich PB, Wright IJ, Cavender-Bares J, et al. 2003. The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Science* **164**: S143–S164.
- Reichard S, Hamilton CW. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* **11**: 193–203.
- Rejmánek M. 2000. Invasive plants: approaches and predictions. *Austral Ecology* **25**: 497–506.
- Rejmánek M, Richardson DM. 1996. What attributes make some plant species more invasive? *Ecology* **77**: 1655–1661.
- Rejmánek M, Richardson DM, Higgins SI, Pitcairn MJ, Grotkopp E. 2005a. Ecology of invasive plants: state of the art. In: Mooney HA, RN Mack, JA McNeely, LE Neville, PJ Schei, Waage J. eds. *Invasive alien species: searching for solutions*. Washington, DC: Island Press, 104–161.
- Rejmánek M, Richardson DM, Pyšek P. 2005b. Plant invasions and invasibility of plant communities. In: van der Maarel E. ed. *Vegetation ecology*. Oxford: Blackwell Science, 332–355.
- Ricciardi A, Cohen J. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* **9**: 309–315.
- Richards CL, Pennings SC, Donovan LA. 2005. Habitat range and phenotypic variation in salt marsh plants. *Plant Ecology* **176**: 263–273.
- 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.
- Richards CL, Walls R, Bailey JP, Parameswaran R, George T, Pigliucci M. 2008. Plasticity in salt tolerance traits allows for invasion of salt marshes by Japanese knotweed *s.l.* (*Fallopia japonica* and *F. ×bohemica*, Polygonaceae). *American Journal of Botany* **95**: 931–942.
- Richards CL, Bossdorf O, Pigliucci M. 2010a. What role does heritable epigenetic variation play in phenotypic evolution? *Bioscience* **60**: 232–237.
- Richards CL, Bossdorf O, Verhoeven KJF. 2010b. Understanding natural epigenetic variation. *New Phytologist* **187**: 562–564.
- Richards EJ. 2008. Population epigenetics. *Current Opinion in Genetics & Development* **18**: 221–226.
- Richardson DM, Pyšek P. 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* **30**: 409–431.
- Richardson DM, Pyšek P, Rejmánek M, Barbour MG, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**: 93–107.
- Rowe CLJ, Leger EA. 2011. Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evolutionary Applications* **4**: 485–498.
- Salmon A, Ainouche ML, Wendel JF. 2005. Genetic and epigenetic consequences of recent hybridization and polyploidy in *Spartina* (Poaceae). *Molecular Ecology* **14**: 1163–1175.
- Sax DF. 2002. Equal diversity in disparate species assemblages: a comparison of native and exotic woodlands in California. *Global Ecology & Biogeography* **11**: 49–58.
- Scharfy D, Funk A, Venterink HO, Gusewell S. 2011. Invasive forbs differ functionally from native graminoids, but are similar to native forbs. *New Phytologist* **189**: 818–828.
- Schierenbeck KA, Mack RN, Sharitz RR. 1994. Effects of herbivory on growth and biomass allocation of native and introduced species of *Lonicera*. *Ecology* **75**: 1661–1672.
- Schutzenhofer MR, Knight TM. 2007. Population-level effects of augmented herbivory on *Lespedeza cuneata*: implications for biological control. *Ecological Applications* **17**: 965–971.
- Sebert-Cuvillier E, Paccaut F, Chabrierie O, Endels P, Goubet O, Decocq G. 2007. Local population dynamics of an invasive tree species with a complex life-history cycle: a stochastic matrix model. *Ecological Modelling* **201**: 127–143.
- Sexton JP, McKay JK, Sala A. 2002. Plasticity and genetic diversity may allow saltcedar to invade cold climates in North America. *Ecological Applications* **12**: 1652–1660.
- Shea K, Kelly D. 1998. Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecological Applications* **8**: 824–832.
- Shea K, Kelly D, Sheppard AW, Woodburn TL. 2005. Context-dependent biological control of an invasive thistle. *Ecology* **86**: 3174–3181.
- Sheppard AW, Hodge P, Paynter Q, Rees M. 2002. Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. *Journal of Applied Ecology* **39**: 721–734.
- Shipley B. 2010. *From plant traits to vegetation structure: chance and selection in the assembly of ecological communities*. Cambridge: Cambridge University Press.
- Simberloff D, Dayan T, Jones C, Ogura G. 2000. Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology* **81**: 2086–2099.
- Stears RJ, Funk JL, Allen EB. 2011. Can resource-use traits predict native vs. exotic plant success in carbon amended soils? *Ecological Applications* **21**: 1211–1224.
- Stock WD, Wienand KT, Baker AC. 1995. Impacts of invading N₂-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ¹⁵N natural abundance values. *Oecologia* **101**: 375–382.
- Suding KN, Lavorel S, Chapin FSIII, et al. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology* **14**: 1125–1140.

- Sultan SE. 2001.** Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* **82**: 328–343.
- Tecco PA, Díaz S, Cabido M, Urceley C. 2010.** Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? *Journal of Ecology* **98**: 17–27.
- Van Valen L. 1965.** Morphological variation and width of ecological niche. *American Naturalist* **99**: 377–390.
- Verhoeven KJF, Jansen JJ, van Dijk PJ, Biere A. 2010.** Stress-induced DNA methylation changes and their heritability in asexual dandelions. *New Phytologist* **185**: 1108–1118.
- Vilá M, Espinar JL, Hejda M, et al. 2011.** Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* **14**: 702–708.
- Vile D, Shipley B, Garnier E. 2006.** A structural equation model to integrate changes in functional strategies during old field succession. *Ecology* **87**: 504–517.
- Violle C, Navas M, Vile D, et al. 2007.** Let the concept of trait be functional! *Oikos* **116**: 882–892.
- Vitousek PM. 1990.** Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* **57**: 7–13.
- Vitousek PM, Walker LR. 1989.** Biological invasion by *Myrica faya*: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* **59**: 247–265.
- Vitousek PM, Walker LR, Whiteaker LD, Mueller-Dombois D, Matson PA. 1987.** Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* **238**: 802–804.
- Von Holle B, Simberloff D. 2005.** Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* **86**: 3212–3218.
- Wallace AR. 1870.** *Contributions to the theory of natural selection*, 2nd edn. 1871. London: MacMillan and Company.
- Weiher E, van der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O. 1999.** Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**: 609–620.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002.** Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**: 125–159.
- Whisenant S. 1990.** *Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications*. General Technical Report INT-276. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station, 1–11.
- Woodward FI, Cramer W. 1991.** Plant functional types and climatic changes: introduction. *Journal of Vegetation Science* **7**: 306–308.
- Woodward FI, Diament AD. 1996.** Functional approaches to predicting the ecological effects of global change. *Functional Ecology* **5**: 202–212.
- Wright IJ, Reich PB, Westoby M, et al. 2004.** The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Wright JP, Naem S, Hector A, et al. 2006.** Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecology Letters* **9**: 111–120.
- Yeh P, Price TD. 2004.** Adaptive phenotypic plasticity and the successful colonization of a novel environment. *American Naturalist* **164**: 531–542.
- Yelenik SG, Stock WD, Richardson DM. 2007.** Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function. *Biological Invasions* **9**: 117–125.
- Zedler JB. 2000.** Progress in wetland restoration ecology. *Trends in Ecology and Evolution* **15**: 402–407.
- Zhang Y-Y, Zhang D-Y, Barrett SCH. 2010.** Genetic uniformity characterizes the invasive spread of water hyacinth (*Eichhornia crassipes*), a clonal aquatic plant. *Molecular Ecology* **19**: 1774–1786.