

SPECIAL FEATURE – EDITORIAL

PLANT FUNCTIONAL EFFECTS ON ECOSYSTEM SERVICES

Plant functional effects on ecosystem services

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Summary

1. The prominent new place of ecosystem services in environmental policy, land management and land planning requires that the best ecological knowledge be applied to ecosystem service quantification. Given strong evidence that functional diversity underpins the delivery of key ecosystem services, assessments of these services may progress rapidly using a trait-based approach.

2. The trait-based approach shows promising results, especially for plant trait effects on primary production and some processes associated with carbon and nitrogen cycling in grasslands. However, there is a need to extend the proof of concept for a wider range of ecosystems and ecosystem services and to incorporate not only the functional characteristics of plants but those of other organisms with which plants interact for the provision of ecosystem services.

3. The five papers in this Special Feature illustrate how some of the key conceptual and methodological challenges can be resolved, and provide a range of case studies across three continents. Relevant plant functional traits depict different axes of variation including stature, the leaf economics spectrum, and associated or independent variations in root or stem traits. The application of the trait approach to ecosystem processes underpinned by interactions between plants and other biota is illustrated for soil micro-organisms and granivorous invertebrates. There is strong evidence for the biomass ratio hypothesis (i.e. prevalent effects of the traits of dominant species through the community-weighted mean), along with less prevalent and more complex effects of heterogeneous trait values between species (i.e. functional divergence).

4. *Synthesis.* Together, the five papers in this Special Feature illustrate how trait-based approaches may help elucidate the complexity of ecological mechanisms operating in the field to determine ecosystem service delivery. To address scientific and management questions about the provision of multiple services, progress is needed in understanding how functional trade-offs and synergies within organisms scale up to interactions between ecosystem services. Service-oriented ecosystem management within the context of global change, or ecological restoration, remains a major challenge, but trait-based understanding opens new avenues towards more generic, integrated approaches.

Key-words: biomass ratio hypothesis, biotic interactions, carbon and nitrogen cycling, ecosystem services, functional variance, insects, multifunctionality soil micro-organisms, plant economics spectrum, plant functional diversity

Introduction

Ecosystem services on which humans depend for their livelihoods, and for their ability to cope with and adapt to global change have recently emerged as a strong element of environmental policy and ecosystem management (Daily *et al.* 2009; Perrings *et al.* 2011). This recognition of ecosystem services has stimulated an exponential increase in research activity in multiple scientific disciplines (Vihervaara, Rönkä & Walls

2010; Seppelt *et al.* 2011), to which ecology needs to make an important contribution. Critical advances are required to support ecosystem services assessments that will be used to inform policy or for the design of land planning, management or ecological restoration strategies. Among these, the inclusion of greater biophysical realism must be a priority in order to go beyond geographical approaches using land cover and a limited number of abiotic or infrastructure characteristics as proxies for ecosystem services (Eigenbrod *et al.* 2010; Lavorel *et al.* 2011; Seppelt *et al.* 2011). Specifically, ecosystem service research needs to incorporate the best ecological knowledge, in order to quantify individual services (Kremen

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2005; Luck *et al.* 2009), to understand mechanisms underpinning ecosystem potential to deliver these services, and to understand synergies and trade-offs between multiple services (Bennett, Peterson & Gordon 2009; Lavorel & Grigulis 2012).

Many components of biodiversity affect ecosystem service delivery (Díaz *et al.* 2006; Cardinale *et al.* 2012; Mace, Norris & Fitter 2012). Among these, functional diversity (FD), broadly defined as the value, range and relative abundance of plant functional traits in a given ecosystem (Díaz & Cabido 2001), has emerged as a key determinant of a variety of ecosystem services, including fodder and wood provision, carbon sequestration, soil nutrient retention, and pollination or biotic control by insects or vertebrates (Díaz *et al.* 2006; De Bello *et al.* 2010). More specifically, recent ecosystem service research has sought to incorporate FD effects on ecosystem properties relevant to ecosystem services (Díaz *et al.* 2007). It has also embraced the response–effect framework (Lavorel & Garnier 2002) to predict ecosystem service changes in response to environmental change through the identification of functional traits that simultaneously determine community responses to environment and ecosystem functioning (Lavorel *et al.* 2011; Luck *et al.* 2012). This approach shows promising results, especially for plant traits in grasslands (Lavorel *et al.* 2011; Minden & Kleyer 2011; Lienin & Kleyer 2012; Laliberté & Tylianakis 2012). Yet, there is further need to extend the proof of concept for a greater diversity of ecosystems and ecosystem services and to incorporate not only the functional characteristics of plants, but those of other organisms with which plants interact for the provision of ecosystem services (De Deyn, Cornelissen & Bardgett 2008; Reiss *et al.* 2009; De Bello *et al.* 2010; Sutherland *et al.* 2013). Most of the ecosystem service literature so far has quantified single or very few ecosystem services (Seppelt *et al.* 2011). However, to address questions on the simultaneous provision of multiple services, that is, multifunctionality, and its management, progress is needed in the understanding of how functional trade-offs and synergies within organisms translate into interactions between ecosystem services (Lavorel & Grigulis 2012).

This Special Feature presents five papers that illustrate recent progress in the use of plant functional approaches to quantify and understand ecosystem service delivery, and its variation within managed landscapes. Together, these papers cover a range of ecosystem services and the variety of mechanisms through which plant functional traits determine ecosystem functioning. They illustrate how some of the key conceptual and methodological challenges can be resolved, and provide a range of supporting case studies across three continents. Dias *et al.* (2013) propose a novel methodological framework for the design of experimental tests of the relative roles of community-weighted mean (CWM) and FD (quantified by functional richness, evenness and divergence) in ecosystem functioning. This framework is illustrated in the case of the effects of leaf nitrogen and phenolics on temperate tree litter decomposition, an important process underpinning carbon sequestration and the maintenance of soil fertility. Conti

& Díaz (2013) test the contributions of CWM and FD for a set of leaf and stem traits in Chaco woodlands from central Argentina, while Butterfield & Suding (2013) examine the influence of these metrics on variations of fodder production and carbon storage in a Californian Mediterranean-climate rangeland. A range of ecosystem processes and services associated with nitrogen cycling are examined by Grigulis *et al.* (2013), who demonstrate for three European grassland sites the relevance of not only the functional composition (CWM and FD) of plants, but also functional parameters of soil micro-organisms. Finally, Storkey *et al.* (2013) further demonstrate the importance of linking functional traits across trophic levels, in the case of cascading effects of land use on arable weed traits, to carabid beetles and to diet provision for United Kingdom farmland birds. In the following, I discuss three of the key cross-cutting issues from these papers. First, they provide evidence for the relevance of the ‘plant economics spectrum’ (Freschet *et al.* 2010) rather than just the leaf economics spectrum (Wright *et al.* 2004), to ecosystem service provision. Second, although they confirm that carbon and nutrient cycling processes are primarily driven by traits of the most abundant (dominant) species (the biomass ratio hypothesis – Grime 1998), they also show new evidence for more complex effects of heterogeneous trait values between species (i.e. functional divergence). Third, they showcase new evidence for the relevance of trait-based analyses to ecosystem services that are underpinned by interactions between plants and, for instance soil microorganisms, or insects (Lavorel *et al.* 2009). I conclude by considering future challenges that trait-based ecosystem service analyses may help to address, including the management of ecosystems towards multifunctionality.

Strong evidence for the role of the plant economics spectrum

The leaf economics spectrum ranges from ‘exploitative’ plants with fast nutrient acquisition and turnover, associated with thinner, nitrogen-rich leaves and fast growth (e.g. high specific leaf area – SLA, high leaf nitrogen concentration – LNC) to ‘conservative’ plants with denser, nutrient-poor leaves and slower growth (e.g. high leaf dry matter content – LDMC, low LNC; Wright *et al.* 2004). In line with recent studies of temperate grassland (Minden & Kleyer 2011; Lienin & Kleyer 2012; Laliberté & Tylianakis 2012), Grigulis *et al.* (2013) demonstrated the strong relevance of the leaf economics spectrum to ecosystem-level processes associated with carbon and nitrogen cycling, including primary production and litter decomposition: communities dominated by exploitative plants were associated with overall faster nutrient turnover – and the opposite was true for communities dominated by conservative plants (Lavorel & Grigulis 2012). This scaling effect from the leaf economics spectrum to carbon (and nitrogen) cycling was, however, not observed either along an altitudinal gradient in a Californian rangeland (Butterfield & Suding 2013) or in the Argentinian Chaco (Conti & Díaz 2013), where instead root density and wood

density respectively were better predictors of production and carbon storage. These results provide support for the hypothesis that plant economics may not only be reflected in leaves, but also in roots and stems at species (Freschet *et al.* 2010) and at community level (Pérez-Ramos *et al.* 2012). However, neither Butterfield & Suding (2013) nor Conti & Díaz (2013) support whole plant coordination and its feeding forward to carbon and nitrogen cycling (Freschet, Aerts & Cornelissen 2012). Root traits are notably under-investigated due to technical difficulties and are often substituted by measurement of leaf traits (Craine 2009). Nevertheless, Grigulis *et al.* (2013) conclude that root traits need to be incorporated, in addition to leaf traits, into further analyses linking community plant functional parameters, microbial functional parameters and nitrogen cycling processes (Orwin *et al.* 2010). Root traits may have more direct ecosystem effects (Butterfield & Suding 2013) and may not always be well correlated with leaf traits (Orwin *et al.* 2010; Fortunel, Fine & Baraloto 2012). Further, although Conti & Díaz (2013) were not able to include root traits in their study, root structural traits may be strongly correlated with stem traits rather than leaf traits in woody plants (Fortunel, Fine & Baraloto 2012).

Overwhelming evidence for the biomass ratio hypothesis and some new evidence for the effects of functional divergence

Díaz *et al.* (2007) proposed a hypothesis-based, stepwise approach to the analysis of FD effects on ecosystem services. This approach makes it possible to successively identify effects of abiotic factors, of trait CWM and variance (e.g. FD) and any residual species-specific effects. While CWM effects support the biomass ratio hypothesis (Grime 1998) that proposes that ecosystem functioning is primarily driven by traits of the most abundant (dominant) species, FD effects suggest non-additive effects among species with different trait values (Petchey & Gaston 2006). Several studies have suggested that plant community trait effects may primarily be attributed to the biomass ratio hypothesis (CWM effects) rather than to non-additive effects (FD effects) (Mokany, Ash & Roxburgh 2008; Laughlin 2011; Lavorel *et al.* 2011), sometimes due to correlation between these two metrics (Dias *et al.* 2013). However, recent studies have reported not only positive FD effects (Schumacher & Roscher 2009; Mouillot *et al.* 2011), but also negative ones (Laliberté & Tylianakis 2012). In this Special Feature, some non-negligible FD effects were also retained in the models of ecosystem services (Butterfield & Suding 2013; Conti & Díaz 2013; Grigulis *et al.* 2013), although their mechanistic explanation is more speculative. Negative FD effects reported for primary production (Conti & Díaz 2013; Grigulis *et al.* 2013) and for soil and total ecosystem carbon (Conti & Díaz 2013) suggest that strong dominance by tall species, rather than a set of coexisting species with diverse heights, results in greatest above- and below-ground production (Laliberté & Tylianakis 2012). In the case of the chaco, these tall species may also have denser wood and greater below-ground production and hence

make a greater contribution to carbon storage. This contrasts with the observation by Butterfield & Suding (2013) that a greater range of heights among rangeland herbs was associated with higher production. Finally, it can only be tentatively hypothesized that greater diversity in plant size (FD for height) and tissue quality (FD for leaf C : N) may translate to a greater diversity in root architectures and carbon and nutrient inputs to soil micro-organisms (Grigulis *et al.* 2013).

Together, these three papers highlight how difficult it is to identify and interpret CWM versus FD effects in the field, even when using advanced statistical tools. Such difficulties justify the experimental approaches with designs aimed at disentangling CWM from FD effects (Dias *et al.* 2013). First, because CWM and FD follow a theoretical bell-shaped relationship, individual studies, especially in the field, are likely to sample portions of the full parameter space, leading to correlated values across these two metrics. This in itself weakens any prospect of identifying FD effects beyond those of CWM. By designing experiments that sample *a priori* independent combinations of CWM and FD, it becomes possible to test their effects independently. Dias *et al.* (2013) demonstrate how this could be applied in the case of litter mixture experiments, where empirical studies have had problems showing consistent positive or negative effects of plant diversity on decomposition (Gartner & Cardon 2004). For instance, it is possible to manipulate species number and relative abundances to assemble litter mixtures with independent combinations of LNC or leaf phenolics concentrations. This approach may also be used *a posteriori* by sampling between, for example, observed grassland plots to select a subset fulfilling the independence criterion.

Plant traits interact with those of other trophic levels in determining ecosystem services

Many ecosystem services rely on interactions between plants and other trophic levels (De Bello *et al.* 2010; Cardinale *et al.* 2012). For example, carbon and nitrogen cycling and the maintenance of a variety of soil functions involve multiple interactions between plants, herbivores, carnivores and soil biota (Bardgett & Wardle 2003; Brussaard, de Ruiter & Brown 2007). Pollination relies on interactions between the diversity of plants, pollinators and the organisms they interact with (e.g. predators; Kremen *et al.* 2007). Combining a multitrophic perspective with a trait-based approach has thus been proposed as the next breakthrough for advancing biodiversity–ecosystem functioning research (Reiss *et al.* 2009). Indeed, recent studies have highlighted the role of functional traits in interactions between trophic levels and their outcomes in terms of ecosystem functioning (Bardgett & Wardle 2003; De Deyn, Cornelissen & Bardgett 2008; Schmitz 2008; De Bello *et al.* 2010). This strongly suggests that the functional models developed for plants, such as the response–effect framework (Lavorel & Garnier 2002), could be extended to multitrophic systems. This novel concept needs to be developed to improve prediction of the effects of environmental change on ecosystem services that depend on biotic interactions.

Grigulis *et al.* (2013) were able for the first time to identify the relative contributions of plant community and microbial functional parameters to ecosystem processes associated with nitrogen cycling. By doing so, they tested the hypothesis that plant traits alone may be poor predictors of below-ground processes (Eviner & Chapin 2003) and that instead linkages between plants and soil microbial communities should be explored. They identified a continuum from standing green biomass and standing litter, linked mostly with plant traits, to potential N mineralization and potential leaching of soil inorganic N, linked mostly with microbial properties. More exploitative species and taller swards, along with soil microbial communities dominated by bacteria, with rapid microbial activities, were linked with greater fodder production. Conversely, dominance by conservative species and soil microbial communities dominated by fungi and slow activity bacteria was usually linked with low production, but provided greater soil carbon storage and nitrogen retention.

Storkey *et al.* (2013) analysed the impact of contrasting management of arable field margins on plant and invertebrate assemblages by quantifying overlaps between plant response traits to disturbance and the abundance of phytophagous invertebrates. Regularly disturbed field margins, characterized by ruderal plant communities with high SLA and low LDMC, supported a greater abundance of invertebrates. These effects were then extended to estimate the corresponding impact on farmland bird populations in terms of amount of resources to feed chicks in the breeding season. Although a fairly simple linear case, this study thus demonstrates the use of plant traits to address processes and ecosystem services that span an entire food chain.

Conclusion

The five papers in this Special Feature demonstrate how parameters characterizing community FD can be used to identify specific mechanisms underpinning the delivery of ecosystem services directly provided by plants, or resulting from plant functional impacts on other trophic levels. Relevant plant functional traits depict different axes of variation including stature, the leaf economics spectrum and associated or independent variations in root or stem traits. Other trophic levels may be characterized by measures of abundance (e.g. insect abundance), by functional group composition (e.g. the relative abundance of soil fungi and bacteria) or by continuous functional traits (e.g. potential activities of bacteria). The investigation of mechanisms associated with dominant traits (CWM), or non-additive (FD) effects is still in its infancy, but these and other recent results provide strong evidence for the biomass ratio hypothesis (CWM), along with less prevalent and more complex FD effects. Together, the five papers illustrate how trait-based approaches may help elucidate the complexity of mechanisms operating in the field. Further, because the same or related traits underpin multiple ecosystem services, trait-based analyses of ecosystem service provision may be combined with fundamental knowledge on plant functional syndromes and trade-offs to advance the understanding

of patterns and mechanisms of multifunctionality (the simultaneous provision of multiple services) and of ecosystem service trade-offs. Simultaneous services being driven by independently varying traits allows for multifunctionality (Lavorel & Grigulis 2012; Butterfield & Suding 2013), while trade-offs such as those captured by the leaf economics spectrum result in trade-offs between services, such as from productivity to carbon and nitrogen retention (Grigulis *et al.* 2013). Service-oriented ecosystem management within the context of global change, or for instance ecological restoration, remains a major challenge, but trait-based understanding opens new avenues towards more generic, integrated approaches.

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References

- Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, **84**, 2258–2268.
- Bennett, E.M., Peterson, G.D. & Gordon, L.J. (2009) Understanding relationships among multiple ecosystem services. *Ecology Letters*, **12**, 1394–1404.
- Brussaard, L., de Ruiter, P.C. & Brown, G.G. (2007) Soil biodiversity for agricultural sustainability *Agriculture, Ecosystems and Environment*, **121**, 233–244.
- Butterfield, B.J. & Suding, K.N. (2013) Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. *Journal of Ecology*, **101**, 9–17.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature*, **486**, 59–67.
- Conti, G. & Díaz, S. (2013) Plant functional diversity and carbon storage – an empirical test in semiarid forest ecosystems. *Journal of Ecology*, **101**, 18–28.
- Craine, J.M. (2009) *Resource Use Strategies of Wild Plants*. Princeton University Press, Princeton, New Jersey.
- Daily, G.C., Polasky, S., Goldstein, J., Kareiva, P.M., Mooney, H.A., Pejchar, L., Ricketts, T.H., Salzman, J. & Shallenberger, R. (2009) Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment*, **7**, 21–28.
- De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M. *et al.* (2010) Functional traits underlie the delivery of ecosystem services across different trophic levels. *Biodiversity and Conservation*, **143**, 2873–2893.
- De Deyn, G.B., Cornelissen, J.H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.
- Días, A.T.C., Berg, M.P., De Bello, F., Van Oosten, A.R., Bila, K. & Moretti, M. (2013) An experimental framework to identify community functional components driving ecosystem processes and services delivery. *Journal of Ecology*, **101**, 29–37.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.
- Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684–20689.
- Díaz, S., Fargione, J., Chapin, F.S.I. & Tilman, D. (2006) Biodiversity Loss Threatens Human Well-Being. *PLoS Biology*, **4**, e277.
- Eigenbrod, F., Armsworth, P.R., Anderson, B.J., Heinemeyer, A., Gillings, S., Roy, D.B., Thomas, C.D. & Gaston, K.J. (2010) The impact of proxy-based methods on mapping the distribution of ecosystem services. *Journal of Applied Ecology*, **47**, 377–385.

- Eviner, V.T. & Chapin, F.S.I. (2003) Biogeochemical interactions and biodiversity. *Global Change and Human Impacts* (eds J.M. Melillo, C.B. Field & B. Moldan), pp. 151–173. Island Press, Washington, District of Columbia.
- Fortunel, C., Fine, P.V.A. & Baraloto, C. (2012) Leaf, stem and root tissue strategies across 758 Neotropical tree species. *Functional Ecology*, **26**, 1153–1161.
- Freschet, G.T., Aerts, R. & Cornelissen, J.H.C. (2012) A plant economics spectrum of litter decomposability. *Functional Ecology*, **26**, 56–65.
- Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. & Aerts, R. (2010) Evidence of the ‘plant economics spectrum’ in a subarctic flora. *Journal of Ecology*, **98**, 362–373.
- Gartner, T.B. & Cardon, Z.G. (2004) Decomposition dynamics in mixed-species leaf litter. *Oikos*, **104**, 230–246.
- Grigulis, K., Lavorel, S., Krainer, U., Legay, N., Baxendale, C., Dumont, M. *et al.* (2013) Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *Journal of Ecology*, **101**, 47–57.
- Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–906.
- Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, **8**, 468–479.
- Kremen, C., Williams, N.E., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R. *et al.* (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, **10**, 299–314.
- Laliberté, E. & Tylianakis, J.M. (2012) Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. *Ecology*, **93**, 145–155.
- Laughlin, D.C. (2011) Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology*, **99**, 1091–1099.
- Lavorel, S. & Garnier, E. (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.
- Lavorel, S. & Grigulis, K. (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *Journal of Ecology*, **100**, 128–140.
- Lavorel, S., Harrington, R., Storkey, J., Díaz, S., Bello, F.d., Bardgett, R.D. *et al.* (2009) How trait linkages within and across trophic levels underlie the vulnerability of ecosystem services. *RUBICODE Report – FP6, Thematic Area: Global Change and Ecosystems*. European Commission, DG Research, Brussels.
- Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Douzet, R. & Pellet, G. (2011) Using plant functional traits to understand the landscape-scale distribution of multiple ecosystem services. *Journal of Ecology*, **99**, 135–147.
- Lienin, P. & Kleyer, M. (2012) Plant trait responses to the environment and effects on multiple ecosystem properties. *Basic and Applied Ecology*, **13**, 301–311.
- Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R. *et al.* (2009) Quantifying the contribution of organisms to the provision of ecosystem services. *BioScience*, **59**, 223–236.
- Luck, G.W., Lavorel, S., McIntyre, S. & Lumb, K. (2012) Extending trait-based frameworks to vertebrates and improving their application to the study of ecosystem services. *Journal of Animal Ecology*, **81**, 1065–1076.
- Mace, G., Norris, K. & Fitter, A.H. (2012) Biodiversity and ecosystem services: a multilayered relationship. *Trends in Ecology and Evolution*, **27**, 19–26.
- Minden, V. & Kleyer, M. (2011) Testing the effect–response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science*, **22**, 387–401.
- Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.
- Mouillot, D., Villéger, S., Scherer-Lorenzen, M. & Mason N.W.H. (2011) Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS ONE*, **6**, e17476.
- Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S. & Bardgett, R.D. (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology*, **98**, 1074–1083.
- Pérez-Ramos, I.M., Roumet, C., Cruz, P., Blanchard, A., Autran, P. & Garnier, E. (2012) Evidence for a ‘plant community economics spectrum’ driven by nutrient and water limitations in a Mediterranean rangeland of southern France. *Journal of Ecology*, **100**, 1315–1327.
- Perrings, C., Duraiappah, A.K., Larigauderie, A. & Mooney, H.A. (2011) The biodiversity and ecosystem services science-policy interface. *Science*, **331**, 1139–1140.
- Petchey, O.L. & Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecology Letters*, **9**, 741–748.
- Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology and Evolution*, **24**, 505–514.
- Schmitz, O.J. (2008) Effects of predator hunting mode on grassland ecosystem function. *Science*, **319**, 952–954.
- Schumacher, J. & Roscher, C. (2009) Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos*, **118**, 1659–1668.
- Seppelt, R., Dormann, C.F., Eppink, F.V., Lautenbach, S. & Schmidt, S. (2011) A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. *Journal of Applied Ecology*, **48**, 630–636.
- Storkey, J., Brooks, D., Haughton, A., Hawes, C., Smith, B.M. & Holland, J. M. (2013) Using functional traits to quantify the value of plant communities to invertebrate ecosystem service providers in arable landscapes. *Journal of Ecology*, **101**, 38–46.
- Sutherland, W.J., Freckleton, R.P., Godfray, H.C.J., Beissinger, S.R., Benton, T., Cameron, D.D. *et al.* (2013) Identification of 100 fundamental ecological questions. *Journal of Ecology*, **101**, 58–66.
- Vihervaara, P., Rönkä, M. & Walls, M. (2010) Trends in ecosystem service research: early steps and current drivers. *AMBIO: A Journal of the Human Environment*, **39**, 314–324.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

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