Journal of Vegetation Science **24** (2013) 942–948

SPECIAL FEATURE: FUNCTIONAL DIVERSITY

A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services

Sandra Lavorel, Jonathan Storkey, Richard D. Bardgett, Francesco de Bello, Matty P. Berg, Xavier Le Roux, Marco Moretti, Christian Mulder, Robin J. Pakeman, Sandra Díaz & Richard Harrington

Keywords
Functional trait; Ecosystem functioning; Biotic interactions; Plant-soil interactions; Biotic control; Environmental change; Pollination; Grassland; Soil nitrogen; Field margins

Received 31 December 2011
Accepted 13 March 2013
Co-ordinating Editor: Norman Mason

Lavorel, S. (corresponding author, sandra.lavorel@ujf-grenoble.fr) & **Díaz, S.** (sdiaz@efn.uncor.edu): Laboratoire d'Ecologie Alpine, CNRS, UMR 5553, Université Joseph Fourier, BP 53 38041, Grenoble Cedex 9, France
Storkey, J. (jonathan.storkey@rothamsted.ac.uk) & **Harrington, R.** (richard.harrington@rothamsted.ac.uk): AgroEcology Department, Rothamsted Research, Harpenden Herts, AL5 2JQ, UK
Bardgett, R.D. (richard.bardgett@manchester.ac.uk): Faculty of Life Sciences, Michael Smith Building, The University of Manchester, Oxford Road, Manchester, M13 9PT, UK
de Bello, F. (fradebello@ctfc.es): Institute of Botany, Academy of Sciences of the Czech Republic, Dukelská 135, CZ-379 82 Třeboň, Czech Republic
Berg, M.P. (m.p.berg@vu.nl): Department of Ecological Science, VU University Amsterdam, De Boelelaan 1085, 1081 HV, Amsterdam, the Netherlands
Le Roux, X. (xavier.le-roux@univ-lyon1.fr): Laboratoire d'Ecologie Microbienne, Université de Lyon, Université Lyon 1, INRA (USC 1193), CNRS (UMR 5557), Bât Mendel, 43 bd du 11 novembre 1918, 69622, Villeurbanne France
Moretti, M. (marco.moretti@wsl.ch): Swiss Federal Research Institute WSL, Community Ecology, Via Belsoggiorno 22, CH-6500, Bellinzona Switzerland
Mulder, C. (christian.mulder@rivm.nl): Centre for Sustainability, Environment and Health, RIVM, Box 1, Bilthoven 3720 BA, the Netherlands
Pakeman, R.J. (robin.pakeman@hutton.ac.uk): The James Hutton Institute, Craigiebuckler, Aberdeen AB15 8QH, UK
Díaz, S. (sdiaz@efn.uncor.edu): IMBIV (CONICET-UNC) and FCEFyN, Universidad Nacional de Córdoba, Casilla de Correo 495, 5000, Córdoba Argentina

Abstract

A novel conceptual framework is presented that proposes to apply trait-based approaches to predicting the impact of environmental change on ecosystem service delivery by multi-trophic systems. Development of the framework was based on an extension of the response–effect trait approach to capture functional relationships that drive trophic interactions. The framework was populated with worked examples to demonstrate its flexibility and value for linking disparate data sources, identifying knowledge gaps and generating hypotheses for quantitative models.

Introduction

Understanding the processes that underpin ecosystem service delivery is crucial if the impact of change on current and future ecosystem services is to be quantified (Kremen 2005; Cardinale et al. 2012). Recent syntheses of empirical studies have highlighted that functional diversity more often determines ecosystem functioning than does species richness *per se* (Díaz et al. 2006). This has led to the development of trait-based approaches designed to identify biotic control over ecosystem service delivery (Díaz et al. 2007; de Bello et al. 2010; Luck et al. 2012; Lavorel 2013), and the mechanisms underpinning synergies and trade-offs among ecosystem services (Lavorel & Grigulis 2012). Quantifying the overlaps or correlations between these 'effect traits' that determine service delivery and the 'response traits' that determine how the functional diversity of a community responds to an environmental driver has been hypothesized as a way of enhancing predictability of ecosystem functioning (Lavorel & Garnier 2002; Suding et al. 2008), known as 'the response–effect model'.

An increasing number of studies support this hypothesis for plant communities. For example, functional traits that determine plant response to resource availability (e.g. specific leaf area, leaf N content, height) also affect the efficiency of key functions such as biomass production (Minden & Kleyer 2011; Pakeman 2011; Laliberté & Tylianakis 2012; Lienin & Kleyer 2012). However, many ecosystem services ultimately rely on interactions between

Journal of Vegetation Science
Doi: 10.1111/jvs.12083

plants and organisms belonging to other trophic levels (Zhang et al. 2007; Cardinale et al. 2012; Mulder et al. 2012), for example the maintenance of soil fertility (Bardgett & Wardle 2003; Brussaard et al. 2007; Schmitz 2008) and pollination (Kremen et al. 2007). Combining a multi-trophic perspective and interaction networks with a trait-based approach has thus been proposed in principle as the next breakthrough for advancing biodiversity–ecosystem functioning research (Reiss et al. 2009).

Here, we present a novel conceptual framework for addressing this research need in practice. The framework explicitly incorporates into the original 'response–effect model', trait linkages of plants with higher trophic levels to capture indirect effects of environmental change on ecosystem services delivered by consumers. The framework represents an important step in moving from qualitative to quantitative predictions of these systems by formulating hypotheses for statistical models, organizing existing data on individual functional linkages within a system and identifying knowledge gaps. As such, the proposed framework is not meant to be a tool for a comprehensive systems' analysis. Rather, it is intended to identify and test key trait-based mechanisms that underlie ecosystem service delivery, with the ultimate objective of quantifying the direction and magnitude of the response of an ecosystem service to environmental change. Unlike food web or interaction network approaches, this trait-based approach does not require a detailed, mechanistic understanding of complex species-specific trophic interactions (Mulder et al. 2012).

The framework

The framework is broken into a series of four sequential steps, although in practice they could be completed in any order. Figure 1 presents a simple case with two trophic levels, where an environmental driver affects trophic level 1 and the ecosystem function of interest is determined by trophic level 2. This would apply to fertilization effects on a plant–herbivore system, with secondary production (e.g. herbivore biomass) as the ecosystem service, or to grassland management effects on a plant–pollinator system with wild flower or crop pollination as the ecosystem service of interest. We use this second example to populate the framework.

First, the relevant trophic levels and groups of organisms are identified along with the traits that are expected to respond directly to the environmental driver of interest. In the example developed in Fig. 1, intensification of grassland leads to decreased plant height, lower leaf dry matter content and a decreased legume component (Garnier et al. 2007). The possible direct effects of management changes on pollinators are not considered explicitly in Fig. 1, but could be incorporated. The second, and most novel, step is to identify the trophic effect and response traits that can be used to quantify functional linkages which cascade through the primary producer community to the consumer ecosystem service providers. In the case of the pollinator example (Fig. 1), there is good agreement that, at species level, floral 'trophic effect traits' including morphology, colour, fragrance and reward to pollinators (Fenster et al. 2004; Ibanez 2012), influence pollinator communities. At the community level, the amount and nature of flowering resources, and their spread over time, are important determinants of pollinator abundance and species diversity, and ultimately of pollination success (Kremen et al. 2007). For instance, higher floral diversity promotes a diversity of functional groups of pollinators (Potts et al. 2003; Fenster et al. 2004). The linkage between floral traits and pollinator traits has been demonstrated at species level, for instance linking proboscis length with nectar holder depth, or with nectar holder depth and width (Stang et al. 2007; Ibanez 2012). The third step in populating the framework is to identify the 'functional effect traits' of the consumer community and appropriate metrics (CWM, functional dissimilarity or, where processes are driven by idiosyncratic species effects, trait attributes for individual species) that determine ecosystem service delivery (Díaz et al. 2007). To our knowledge, such an analysis has not yet been carried out at community level for pollination services; although there is evidence that increased functional diversity of pollinator communities can increase pollination success (Bluethgen & Klein 2011).

The final step is to identify linkages between response and effect traits within each trophic level to predict the likelihood of the driver of change impacting on service delivery. A study quantifying the effects of habitat management on pollinators found that the assemblage of bee communities responded to the CWMs of flower colour and forage index (Carvel et al. 2006). These, in turn, appear to be correlated with plant response traits via phylogenetic effects such as the presence of specific families/growth forms (Pakeman & Stockan 2013). Although pollinator traits were not included in these previous studies, it is likely that there will be functional differences between bee communities in terms of trophic response and pollination efficiency. For example, if management selects for short-tongued bees, pollination services for plants requiring long-tongued species will decline. If this is found to be the case, predictions of the impact of management on pollinator services based on the direct effects on pollinator abundance alone may differ from models that include the indirect effects of plant traits on pollinator function. However, this level of understanding of the system will require more comprehensive data on the relevant plant effect and bee response traits and their coupling.

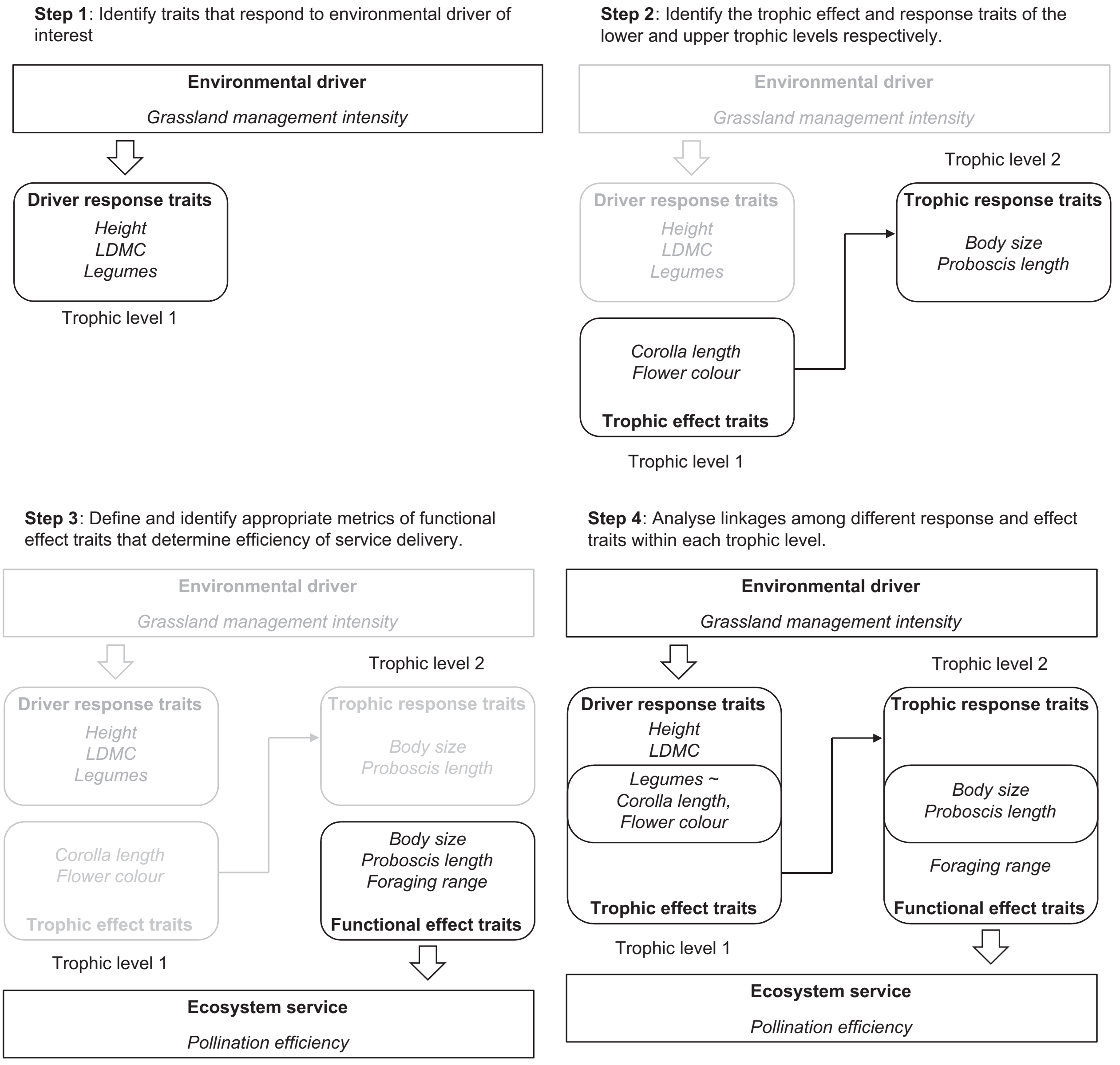

Fig. 1. Method for articulating functional responses and effects within and across two trophic levels to predict changes in ecosystem functioning, and methodological steps for its application. Step 1 identifies response traits for each of the trophic levels to the environmental driver of interest. In this case, only effects on the plants are considered. Within each trophic level *i*, the response of organisms to the environmental driver can be related to particular functional traits (*driver response traits*). Step 2 identifies the *trophic effect traits* of a lower trophic level which affect the next trophic level up, and the corresponding *trophic response traits* of the upper trophic level. Step 3 defines the identity and appropriate metrics of the *functional effect traits* contributing to the ecosystem function. Step 4 analyses linkages among the different response and effect traits within each trophic level. Such linkages can occur through direct overlap (response trait = effect trait) or through association (indicated by ~), e.g. where traits are linked through evolutionary trade-offs.

The framework is intended to be used as a conceptual tool to identify relevant traits and integrate data from disparate studies on individual linkages, and to generate hypotheses on the response of the whole system to given drivers, which can lead to quantitative models. Structural equation modelling (SEM), or path analysis, is a powerful tool to challenge these hypotheses (Shipley 2000). SEMs have recently been applied to test response–effect linkages for plants, making it possible to confirm the pivotal role of plant height and the leaf economics spectrum as linkages between abiotic and management factors, and a variety of ecosystem processes involved in carbon and nitrogen

Journal of Vegetation Science
Doi: 10.1111/jvs.12083

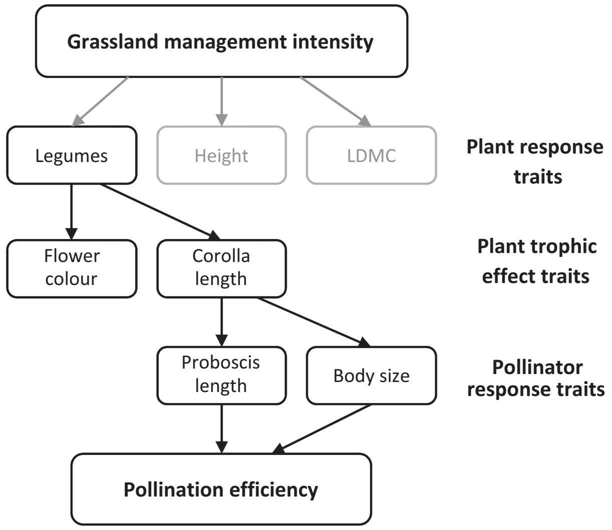

Fig. 2. Hypothesis for a structural equation model (SEM) depicting effects of grassland management intensity on pollination. The SEM tests how management effects on plant traits feed forward to pollinator traits involved in pollination efficiency. Plant height and leaf dry matter concentration (LDMC) would not be retained in the final model given their lack of direct links with floral traits relevant to pollinators. Black arrows indicate positive effects; grey arrows indicate negative effects.

cycling (Minden & Kleyer 2011; Laliberté & Tylianakis 2012; Lavorel & Grigulis 2012; Lienin & Kleyer 2012).

Figure 2 illustrates a possible hypothesis for a SEM of the impact of grassland intensification on wild flower or crop pollination mediated by plant–pollinator functional interactions derived from the framework illustrated in Fig. 1. To date, this approach has only been used to test the framework in its comprehensive form in an analysis of coupled plant- and grasshopper-trait effects on primary productivity (Moretti et al. 2013). A combination of univariate and multivariate approaches was used first to select traits relevant to grassland management response (step 1), to plant–grasshopper interactions (step 2), and to primary production (step 3), while linkages flowing through the two trophic levels were identified manually as both responding to management and/or the other trophic level and traits affecting primary production (step 4). The two functional metrics thus retained, i.e. CWM leaf dry matter concentration (LDMC) and CWM body mass, were then used to build a structural equation model demonstrating the effects of management on primary production, both directly through CWM LDMC, and indirectly through the effects of these plant metrics on CWM body mass. The fact that the final SEM retained the path through grasshopper body mass and its response to plant LDMC, rather than only a direct path through plant traits, provides strong evidence for the relevance of using our framework which included a quantification of the trophic path, and thereby of biomass consumption by grasshoppers proportional to their body size.

Discussion

The example developed in Fig. 1 has a single driver of change and two trophic levels. However, the modular structure of the framework means that it has the flexibility to incorporate more than two trophic levels or multiple services and drivers. Two examples from temperate agro-ecosystems, for which extensive knowledge can be synthesized from the literature, have been developed in Appendix S1 (Supporting Information) to demonstrate this flexibility. They illustrate the potential of the framework for articulating often fragmented knowledge from complex systems into a comprehensive analysis. The first example shows how, by introducing traits explicitly for the soil microbial component, the application of the framework provides a conceptual basis for testing the mechanisms that underpin a well-known feedback loop of the nitrogen cycle involving plants and soil micro-organisms. This example also highlights the potential to incorporate the direct impact of the environmental driver on multiple trophic levels. The second example demonstrates how the framework can support the analysis of trait-based trade-offs and synergies among multiple ecosystem services using the functional composition of the plant community to integrate functions. Although both examples only include a single driver of change, in many cases several drivers, such as land use and climate change, are likely to interact with unpredictable effects on biotic interactions and the functions that they drive (Tylianakis et al. 2008). In such cases the framework would be used to identify multiple groups of response traits and analyse independence or association among them as well as their linkages with effects traits of interest.

In applying the framework to multiple case studies, the authors encountered a number of constraints. First, although linear interaction networks are relatively straightforward to formulate using the framework, difficulties arise as more trophic levels, with intrinsic feedbacks, are added (e.g. the full decomposer food web) unless there is a clear effect of ecosystem engineers (e.g. earthworms) that overrides all other trophic groups (Lavorel et al. 2009). Future applications of the framework should explore its value and limits for more complex cases (Mulder et al. 2012). Second, the framework is most suited to addressing processes operating at local scale. Addressing services depending on non-linear spatial processes, whether for ecosystem fluxes or for the dynamics of ecosystem service-providing organisms (e.g. Woodcock et al. 2010), will require that the framework be used in conjunction with spatial theory (Fahrig et al. 2011), and that relevant traits such as dispersal ability are incorporated (Kremen et al. 2007). This represents a key research frontier at the intersection of trait-based functional ecology, community ecology and landscape ecology (see e.g. Kennedy et al. 2010; Öckinger et al. 2010). Finally, current knowledge on traits for biota other than plants remains a constraint for the application of the framework and to the development of corresponding quantitative analyses. Attempts to apply the framework will guide the production of the necessary trait lists and measurement methodologies (Cornelissen et al. 2003), and hopefully, in time, of shared databases (Kattge et al. 2011).

Acknowledgements

This work was supported by the RUBICODE Coordinated Action (Rationalising Biodiversity Conservation in Dynamic Ecosystems) of FP6 of the European Commission (Contract No. 036890). RUBICODE contributes to the Global Land Project. We are grateful to Marie Vandewalle for help in preparation of the workshop that led to development of these ideas. Pablo Cipriotti, Hans Cornelissen, Christian Feld, Sylvain Dolédec, Thierry Hance, Jan Lepš, Juliet Osborne, Peter Poschlod and Simon Potts provided valuable input during the successive refinements of the framework.

References

Bardgett, R.D. & Wardle, D.A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84: 2258–2268.

Bluethgen, N. & Klein, A.-M. 2011. Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology* 12: 282–291.

Brussaard, L., De Ruiter, P.C. & Brown, G.G. 2007. Soil biodiversity for agricultural sustainability. *Agriculture, Ecosystems and Environment* 121: 233–244.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauderie, A., Srivastava, D.S. & Naeem, S. 2012. Biodiversity loss and its impact on humanity. *Nature* 486: 59–67.

Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D. & Goulson, D. 2006. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* 132: 481–489.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. 2003. Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.

de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J.H.C., Bardgett, R.D., Berg, M.P., Cipriotti, P., Feld, C.K., Hering, D., Da Silva, P.M., Potts, S.G., Sandin, L., Sousa, J.P., Storkey, J., Wardle, D.A. & Harrison, P.A. 2010. Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation* 19: 2873–2893.

Díaz, S., Fargione, J., Chapin, F.S. III & Tilman, D. 2006. Biodiversity loss threatens human well-being. *PLoS Biology* 4: e277.

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 of the United States of America* 104: 20684–20689.

Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M. & Martin, J.-L. 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters* 14: 101–112.

Fenster, C.B., Armbruster, W.S., Wilson, P., Dudash, M.R. & Thomson, J.D. 2004. Pollination syndromes and floral specialization. *Annual Review of Ecology and Systematics* 35: 375–403.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Leps, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V., Quested, H., Quétier, F., Robson, T.M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thébault, A., Vile, D. & Zarovali, M.P. 2007. A standardized methodology to assess the effects of land use change on plant traits, communities and ecosystem functioning in grasslands. *Annals of Botany* 99: 967–985.

Ibanez, S. 2012. Optimizing size thresholds in a plant–pollinator interaction web: towards a mechanistic understanding of ecological networks. *Oecologia* 170: 233–242.

Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., Van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., Ackerly, D.D., Anand, M., Atkin, O., Bahn, M., Baker, T.R., Baldocchi, D., Bekker, R., Blanco, C.C., Blonder, B., Bond, W.J., Bradstock, R., Bunker, D.E., Casanoves, F., Cavender-Bares, J., Chambers, J.Q., Chapin, F.S. III, Chave, J., Coomes, D., Cornwell, W.K., Craine, J.M., Dobrin, B.H., Duarte, L., Durka, W., Elser, J., Esser, G., Estiarte, M., Fagan, W.F., Fang, J., Fernández-Méndez, F., Fidelis, A., Finegan, B., Flores, O., Ford, H., Frank, D., Freschet, G.T., Fyllas, N.M., Gallagher, R.V., Green, W.A., Gutierrez, A.G., Hickler, T., Higgins, S.I., Hodgson, J.G., Jalili, A., Jansen, S., Joly, C.A., Kerkhoff, A.J., Kirkup, D., Kitajima, K., Kleyer, M., Klotz, S., Knops, J.M.H., Kramer, K., Kühn, I., Kurokawa, H., Laughlin, D., Lee, T.D., Leishman, M., Lens, F., Lenz, T., Lewis, S.L., Lloyd, J., Llusià, J., Louault, F., Ma, S., Mahecha, M.D., Manning, P., Massad, T., Medlyn, B.E., Messier, J., Moles, A.T., Müller, S.C., Nadrowski, K., Naeem, S., Niine-

Doi: 10.1111/jvs.12083

mets, Ü., Nöllert, S., Nüske, A., Ogaya, R., Oleksyn, J., Onipchenko, V.G., Onoda, Y., Ordoñez, J., Overbeck, G., Ozinga, W.A., Patiño, S., Paula, S., Pausas, J.G., Peñuelas, J., Phillips, O.L., Pillar, V., Poorter, H., Poorter, L., Poschlod, P., Prinzing, A., Proulx, R., Rammig, A., Reinsch, S., Reu, B., Sack, L., Salgado-Negret, B., Sardans, J., Shiodera, S., Shipley, B., Siefert, A., Sosinski, E., Soussana, J.-F., Swaine, E., Swenson, N., Thompson, K., Thornton, P., Waldram, M., Weiher, E., White, M., White, S., Wright, S.J., Yguel, B., Zaehle, S., Zanne, A.E. & Wirth, C. 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.

Kennedy, C.M., Marra, P.P., Fagan, W.F. & Neel, M.C. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs* 80: 651–669.

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., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vasquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J. & Rickletts, T.H. 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.

Lavorel, S. 2013. Plant functional effects on ecosystem services. *Journal of Ecology* 101: 4–8.

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., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Douzet, R. & Pellet, G. 2009. 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., 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.

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.

Moretti, M., de Bello, F., Ibanez, S., Fontana, S., Pezzatti, G.B., Dziock, F., Rixen, C. & Lavorel, S. 2013. Linking traits between plants and invertebrate herbivores to track functional effects of environmental changes. *Journal of Vegetation Science* 24: 949–962.

Mulder, C., Boit, A., Mori, S., Vonk, J.A., Dyer, S.D., Faggiano, L., Geisen, S., González, A.L., Kaspari, M., Lavorel, S., Marquet, P.A., Rossberg, A.G., Sterner, R.W., Voigt, W. & Wall, D.H. 2012. Distributional (in) congruence of Biodiversity–Ecosystem Functioning. *Advances in Ecological Research* 46: 1–88.

Öckinger, E., Schweiger, O., Crist, T.O., Debinski, D.M., Krauss, J., Kuussaari, M., Petersen, J.D., Pöyry, J., Settele, J., Summerville, K.S. & Bommarco, R. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. *Ecology Letters* 13: 969–979.

Pakeman, R.J. 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology* 92: 1353–1365.

Pakeman, R.J. & Stockan, J. 2013 Using plant functional traits as a link between land use and bee foraging abundance. *Acta Oecologica* 50: 32–39.

Potts, S.G., Vulliamy, B., Dafni, A., Ne'eman, G. & Willmer, P. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84: 2628–2642.

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* 24: 505–514.

Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. *Science* 319: 952–954.

Shipley, B. 2000. *Cause and correlation in ecology – A user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge, UK.

Stang, M., Klinkhamer, P. & Van der Meijden, E. 2007. Asymmetric specialization and extinction risk in plant–flower visitor webs: a matter of morphology or abundance? *Oecologia* 151: 442–453.

Suding, K.N., Lavorel, S., Chapin, F.S. III, Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.L. 2008. Scaling environmental change from traits to communities to ecosystems: the challenge of intermediate-level complexity. *Global Change Biology* 14: 1125–1140.

Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. 2008. Global change and species interactions in terrestrial ecosystems. *Ecology Letters* 11: 1351–1363.

Woodcock, B.A., Redhead, J., Vanbergen, A.J., Hulmes, L., Hulmes, S., Peyton, J., Nowakowski, M., Pywell, R.F. & Heard, M.S. 2010. Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agriculture, Ecosystems and Environment* 139: 181–186.

Zhang, W., Ricketts, T.H., Kremen, C., Carney, K. & Swinton, S.M. 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics* 64: 253–260.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Formalizing available knowledge into the framework.

Figure S1. Framework implementation for analysing the effects of changes in the intensity of grassland management through grazing and its influence on soil N provision via N transformations.

Figure S2. Using trait linkages to assess the impact of field margin management on multiple ecosystem services.

Doi: 10.1111/jvs.12083