Received: 18 September 2017 | Accepted: 22 January 2018
DOI: 10.1111/1365-2664.13129

COMMENTARY

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Fertilising semi-natural grasslands may cause long-term negative effects on both biodiversity and ecosystem stability

Indrek Melts[1] | Kaire Lanno[2] | Marek Sammul[3] | Kei Uchida[4] | Katrin Heinsoo[2] | Tiiu Kull[2] | Lauri Laanisto[2]

[1]Integrated Research System for Sustainability Science (IR3S), The University of Tokyo, Tokyo, Japan

[2]Chair of Biodiversity and Nature Tourism, Estonian University of Life Sciences, Tartu, Estonia

[3]Chair of Natural Resources, University of Tartu, Tartu, Estonia

[4]Graduate School of Environment and Information Sciences, Yokohama National University, Yokohama, Japan

Correspondence
Indrek Melts
Email: indrek.melts@gmail.com

Funding information
Postdoctoral Fellowship of Japan Society for the Promotion of Science, Grant Number: JP16F16755; Estonian Research Council, Grants Number: IUT 21-1, IUT 34-7, PUT 1409 and PUT 1463

Handling Editor: Kechang Niu

Abstract

1. Some short-term experiments in applied ecology and agricultural research have demonstrated that nutrient applications in semi-natural grasslands can maintain productivity and will not result in the decrease of plant species richness. Such findings may have an impact on management choices and quality of valuable plant communities, and therefore, further discussion of this topic is necessary.
2. We highlight three aspects regarding the management suggestions in grassland communities with high biodiversity: (1) short-term study results may not reflect potential long-term changes; (2) broad range of grasslands may respond to disturbance in site specific ways; and (3) practical advices should contain careful consideration of existing ecological literature regarding grassland management and sustainable biodiversity.
3. *Synthesis and applications*. Considering effects of fertilisation on biodiversity, we argue against nutrient application to semi-natural grasslands. Biodiversity supports the resilience of grassland ecosystems and maintains a stable biomass yield. Current short-term experiments are good indicators about the need for a long-term experiments and meta-analysis for detailed understanding of ecosystem functions in different types and areas during global change.

KEYWORDS
biodiversity, bioeconomy, ecosystem services, fertilisation, grassland, nutrient-rich residues, productivity, species richness

1 | INTRODUCTION

Recently, the use of nutrient-rich residues from bioenergy production (digestate) and intensive husbandry (slurry) for fertilising traditionally managed grasslands has gained increased attention (e.g. Duffková, Hejcman, & Libichová, 2015; Duffková & Libichová, 2013; Hensgen, Bühle, & Wachendorf, 2016; Kováčiková, Vargová, & Jančová, 2013). Hensgen et al. (2016) used low-dose nutrient applications (i.e. 25–54 kg N ha^{-1} $year^{-1}$, 2–5 kg P ha^{-1} $year^{-1}$ and 20–51 kg K ha^{-1} $year^{-1}$ for 5 years) in semi-natural grasslands to maintain productivity and claimed that these applications did not result in a loss of species richness during the 5-year study. Similar short-term experiments by Duffková and Libichová (2013) and Duffková et al. (2015) came to similar conclusions: low-dose cattle slurry application (i.e. 0–240 kg N ha^{-1} $year^{-1}$ and 0–240 kg N ha^{-1} $year^{-1}$, 0–40 kg P ha^{-1} $year^{-1}$ and 0–180 kg K ha^{-1} $year^{-1}$ for 6 years, respectively) increases the herbage yield without affecting the diversity in a species-rich grassland.

The use or recommendation of new intensive management strategies in semi-natural grasslands is complicated. Such complexity is typical in ecosystems with high biodiversity and conservation values (e.g. Veen, Jefferson, de Smidt, & Van der Straaten, 2009). Generally, fertilisation decreases plant diversity and changes the species composition (Bobbink, Hornung, & Roelofs, 1998; Borer et al., 2014; De Schrijver et al., 2011; Isbell et al., 2013; Kidd, Manning, Simkin, Peacock, & Stockdale, 2017; Kleijn et al., 2009; Suding et al., 2005; Tilman, 1987; Zhang, Zhou, Li, Guo, & Du, 2015). The negative effects on biodiversity have been reported also for cases of low nitrogen addition rates (Clark & Tilman, 2008; Kidd et al., 2017). The experimental N addition load by Clark and Tilman (2008) was 10 kg N ha^{-1} $year^{-1}$ over 8 years and 120 years long fertilisation was of 35 kg N ha^{-1} $year^{-1}$ plus grazing of cattle or sheep.

Therefore, we express our concerns about results claiming that species-rich grasslands can be fertilised to maintain or increase above-ground productivity without negatively affecting plant diversity and that these methods can be widely applied for the management of semi-natural meadows. Such studies in the future should critically consider existing ecological literature related to productivity and biodiversity. Here, we note three core issues that can influence the results and should be reflected in future studies in this research area: the duration of the experiment, site-specific characteristics and the theoretical background.

2 | DURATION OF EXPERIMENTS

Numerous long-term studies have confirmed that fertilisation negatively affects species richness and positively influences biomass production. In some cases, negative effects appear rapidly, and in other cases, these effects take time (Dickson & Gross, 2013; Silvertown et al., 2006; Tilman et al., 1994). Yet, changes in community level dynamics continue long after fertilisation ceases, as shown in the long-running Park Grass experiment (established in 1856), in which different organic fertilisers have resulted in slight but notable increases in productivity. However, the effect on species richness has been strongly negative, even decades after the end of fertilisation (Silvertown et al., 2006). Recently, a slight recovery was noted in the plots of the Park Grass experiment where fertilisation treatment had ended, but the diversity there was still lower than in non-fertilised plots (Storkey et al., 2015).

The studies discussed above note the possibility of the low-dose application of nutrients in semi-natural grasslands without causing a loss in diversity. However, since they are based on short-term experiments, they might underestimate the long-term changes in vegetation dynamics and processes (e.g. Mašková, Doležal, Kvet, & Zemek, 2009; Van der Maarel & Sykes, 1993). Furthermore, species composition changes induced by shifts in grassland management can take up to 50 years to appear (see Helm, Hanski, and Pärtel 2006 and related studies on extinction debt). Moreover, changes in these degradation processes or the restoration of original species richness can take even longer (e.g. Hejcman, Klaudisová, Schellberg, & Honsová, 2007; Wortley, Hero, & Howes, 2013).

3 | SITE-SPECIFIC CHARACTERISTICS

The response of each plant community to an environmental change depends on the set of conditions under which it has developed. These conditions differ by habitat, management regime and region (e.g. Biondi et al., 2012; Grévilliot, Krebs, & Muller, 1998; Socher et al., 2013). Meadows are strongly human dependent, and they are not ecologically stable. Even the temporary abandonment of management activities (e.g. Galvánek & Lepš, 2008; Pykälä, Luoto, Heikkinen, & Kontula, 2005; Uchida & Ushimaru, 2014) or the incidental or irregular management of productivity (e.g. Van der Hoek, Mierlo Anita, & Groenendael, 2004) can lead to long-term changes in the species composition. To an extent, mowing may balance the negative effect of fertilisation on species richness in the short term (Lepš, 2014), especially after a period without mowing prior to the start of the experiment (e.g. Liira et al., 2012). Therefore, it is essential to know the previous management strategy of a site. These strategies are independent of the experimental layout, and the response to management changes may depend on the local historical context. Furthermore, extremely nutrient-poor (e.g. dry calcareous grasslands) and most small-scale species-rich habitats (e.g. wooded meadow) should be excluded from such studies, as the negative effects on these plant communities are often extensive (e.g. Johansson et al., 2008; Sammul, Kull, & Kattai, 2013).

One can presume that fertilisation is not new to most of these study sites, and fertilisation-sensitive species may have already disappeared, thereby reducing the original species richness. Additionally, this assumption is supported by considering the species richness reported in the studies of Duffková et al. (2015) and Hensgen et al. (2016). In the first study, the mean number of species was 19.7 per 1 m^2 in all treatments and years, and in the second study, approximately 40 species were observed in different treatments in a 25 m^2 plot. A recent global meta-experiment on the relationship between grassland diversity and productivity (Fraser et al., 2015) reported that the average species richness at the 5 × 5 m scale was approximately 40 species, although the study included several sites with extremely low diversity, including some wetland ecosystems with just a single species. Therefore, although the grasslands studied by Hensgen et al. (2016) and Duffková et al. (2015) were considered species rich by the authors, in comparison with global assessments of similar types of grasslands, for example, Fraser et al. (2015), these communities have average plant diversity at best (see also Chytrý et al., 2015; Wilson, Peet, Dengler, & Pärtel, 2012). Local extinctions of the most sensitive species may have occurred before the experiment began; thus, the effect of fertilisation on diversity is not fully studied under appropriate conditions. One option of estimating the number of species already missing from the community is the “dark diversity” approach (Pärtel, Szava-Kovats, & Zobel, 2011).

4 | THEORETICAL BACKGROUND

Numerous studies have shown that the productivity of species-rich, semi-natural grasslands can remain stable with traditional extensive management (i.e. no additional fertilisation, removal of nutrients via herding or mowing) over time (e.g. Hansson & Fogelfors, 2000;

Sammul et al., 2013; Smits, Willems, & Bobbink, 2008; Tilman, Isbell, & Cowles, 2014). Haying removes nitrogen that would otherwise accumulate in the system (Tilman & Isbell, 2015) and increases light availability (Hautier, Niklaus, & Hector, 2009), both of which promote the coexistence of different and high numbers of herbaceous plant species (e.g. Dengler, Janišová, Török, & Wellstein, 2014). Nutrient addition studies, however, have reported negative effects on diversity in many long-term ecological experiments in grasslands (e.g. Crawley et al., 2005; Hejcman et al., 2007; Isbell et al., 2013; Kidd et al., 2017; Liira et al., 2012; Silvertown et al., 2006; Tilman et al., 2014). Nutrient inputs might increase the biomass of non-native and often generalist species (Brian Patrick, Fraser, & Kershner, 2008) and significantly decrease rare, threatened and specialist species (Kleijn et al., 2009; Uematsu & Ushimaru, 2013). A decrease in species richness can also be a consequence of cumulative N inputs (De Schrijver et al., 2011). As stated previously, the negative effects of nitrogen on the plant species diversity have been confirmed at low fertilisation rates (Bobbink et al., 1998; Clark & Tilman, 2008). Additionally, the decline in plant species richness as nitrogen inputs increased was observed to be linear (Crawley et al., 2005) or logarithmic (Clark & Tilman, 2008).

Concentrating grassland management efforts on maximising the productivity through fertilisation is a short-sighted approach. The key to efficient and steady grassland ecosystem functioning is in maintaining and increasing biodiversity (Hooper et al., 2012; Tilman et al., 2014; Weisser et al., 2017). Species-rich communities have high nutrient use efficiencies, thereby providing stable biomass production compared to species-poor grasslands (e.g. Gross et al., 2014; Isbell et al., 2013; Tilman et al., 2014).

Hence, it is important to maintain regular management via grazing or mowing to preserve species diversity (Pärtel, Bruun, & Sammul, 2005). Instead of fertiliser addition, the removal of aboveground biomass is important for the sustained diversity of high-level plant species (Jacquemyn, Brys, & Hermy, 2003) and the stability of the biomass yield in grasslands (Hautier et al., 2014, 2015; Isbell et al., 2015; Silvertown et al., 2006; Tilman et al., 2014). It is important to decrease the amounts of nutrient-rich residues from biobased production via increasing the resource usage and technological efficiency throughout the biomass-to-bioproducts value chain. Surplus residues could be applied to intensively managed agricultural fields instead of mineral fertilisers but not to extensively managed semi-natural grasslands with nature conservation values.

5 | CONCLUSIONS

Studies focusing on the management of semi-natural communities and use of grassland ecosystems (including the application of new and more efficient technologies) are welcomed, as they are important contributions for both the conservation of these communities and the emerging resource-efficient bioeconomy (e.g. Burrascano et al., 2016). Furthermore, we should identify the relationships between fertilisation and organisms of different trophic levels (e.g. pollinators), as many of these relationships remain unknown (e.g. Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). Our intention in this paper is to emphasise that the long-term effects of fertilisation on community biodiversity and productivity, and especially the stability of ecosystem services, are generally negative. Additionally, overcoming the unfavourable effects of unsound management practices might take several generations. While many semi-natural grasslands require restoration and management efforts to restore their high nature conservation values, it seems unreasonable to include these areas as a part of residue utilisation systems considering the aforementioned potential negative effects. We strongly recommend that the knowledge gained from long-term fertilisation experiments in ecology be considered before applying any additional nutrients to semi-natural grasslands.

ACKNOWLEDGEMENTS

Authors acknowledge support from the Japan Society for the Promotion of Science Postdoctoral Fellowship under the Grant-in-Aid program (no. JP16F16755) and grants IUT 21-1, IUT 34-7, PUT 1409 and PUT 1463 from the Estonian Research Council. We thank Mohan Geetha and Eike Eller for providing general remarks and Wiley Editing Services for language correction. We acknowledge Kechang Niu and two anonymous reviewers.

AUTHORS' CONTRIBUTIONS

I.M. and L.L. conceived and designed the research. I.M., K.L. and L.L. led the writing of this manuscript. All authors participated in writing and critically contributed to the manuscript. All authors have approved the final manuscript for publication.

DATA ACCESSIBILITY

Data have not been archived because this article does not use data.

ORCID

Indrek Melts http://orcid.org/0000-0003-3097-9152

REFERENCES

Biondi, E., Burrascano, S., Casavecchia, S., Copiz, R., Del Vico, E., Galdenzi, D., … Zivkovic, L. (2012). Diagnosis and syntaxonomic interpretation of Annex I Habitats (Dir. 92/43/EEC) in Italy at the alliance level. *Plant Sociology*, *49*, 5–37. https://doi.org/10.7338/pls2012491/01

Bobbink, R., Hornung, M., & Roelofs, J. G. M. (1998). The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *Journal of Ecology*, *86*, 717–738. https://doi.org/10.1046/j.1365-2745.1998.8650717.x

Borer, E. T., Seabloom, E. W., Gruner, D. S., Harpole, W. S., Hillebrand, H., Lind, E. M., … Yang, L. H. (2014). Herbivores and nutrients control grassland plant diversity via light limitation. *Nature*, *508*, 517–520. https://doi.org/10.1038/nature13144

Brian Patrick, L., Fraser, L. H., & Kershner, M. W. (2008). Large-scale manipulation of plant litter and fertilizer in a managed successional temperate grassland. *Plant Ecology*, *197*, 183–195. https://doi.org/10.1007/s11258-007-9369-7

Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luyssaert, S., Sabatini, F. M., & Blasi, C. (2016). Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. *Biological Conservation*, *201*, 370–376. https://doi.org/10.1016/j.biocon.2016.08.005

Chytrý, M., Dražil, T., Hájek, M., Kalníková, V., Preislerová, Z., Šibíik, J., … Vymazalová, M. (2015). The most species-rich plant communities in the Czech Republic and Slovakia (with new world records). *Preslia*, *87*, 217–278.

Clark, C. M., & Tilman, D. (2008). Loss of plant species after chronic low-level nitrogen deposition to prairie grasslands. *Nature*, *451*, 712–715. https://doi.org/10.1038/nature06503

Crawley, M. J., Johnston, A. E., Silvertown, J., Dodd, M., de Mazancourt, C., Heard, M. S., … Edwards, G. R. (2005). Determinants of species richness in the park grass experiment. *The American Naturalist*, *165*, 179–192. https://doi.org/10.1086/427270

De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K., & Verheyen, K. (2011). Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography*, *20*, 803–816. https://doi.org/10.1111/j.1466-8238.2011.00652.x

Dengler, J., Janišová, M., Török, P., & Wellstein, C. (2014). Biodiversity of Palaearctic grasslands: A synthesis. *Agriculture, Ecosystems & Environment*, *182*, 1–14. https://doi.org/10.1016/j.agee.2013.12.015

Dickson, T. L., & Gross, K. L. (2013). Plant community responses to long-term fertilization: Changes in functional group abundance drive changes in species richness. *Oecologia*, *173*, 1513–1520. https://doi.org/10.1007/s00442-013-2722-8

Duffková, R., Hejcman, M., & Libichová, H. (2015). Effect of cattle slurry on soil and herbage chemical properties, yield, nutrient balance and plant species composition of moderately dry Arrhenatherion grassland. *Agriculture, Ecosystem & Environment*, *213*, 281–289. https://doi.org/10.1016/j.agee.2015.07.018

Duffková, R., & Libichová, H. (2013). Effects of cattle slurry application on plant species composition of moderately moist Arrhenatherion grassland. *Plant Soil and Environment*, *59*, 485–491.

Fraser, L. H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., … Zupo, T. (2015). Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science*, *349*, 302–305. https://doi.org/10.1126/science.aab3916

Galvánek, D., & Lepš, J. (2008). Changes of species richness pattern in mountain grasslands: Abandonment versus restoration. *Biodiversity and Conservation*, *17*, 3241–3253. https://doi.org/10.1007/s10531-008-9424-2

Grévilliot, F., Krebs, L., & Muller, S. (1998). Comparative importance and interference of hydrological conditions and soil nutrient gradients in floristic biodiversity in flood meadows. *Biodiversity and Conservation*, *7*, 1495–1520. https://doi.org/10.1023/A:1008826629011

Gross, K., Cardinale, B. J., Fox, J. W., Gonzalez, A., Loreau, M., … Van Ruijven, J. (2014). Species richness and the temporal stability of biomass production: A new analysis of recent biodiversity experiments. *The American Naturalist*, *183*, 1–12. https://doi.org/10.1086/673915

Hansson, M., & Fogelfors, H. (2000). Management of a semi-natural grassland; results from a 15-year-old experiment in southern Sweden. *Journal of Vegetation Science*, *11*, 31–38. https://doi.org/10.2307/3236772

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, *324*, 636–638. https://doi.org/10.1126/science.1169640

Hautier, Y., Seabloom, E. W., Borer, E. T., Adler, P. B., Harpole, W. S., Hillebrand, H., … Hector, A. (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*, *508*, 521–525. https://doi.org/10.1038/nature13014

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, *348*, 336–340. https://doi.org/10.1126/science.aaa1788

Hejcman, M., Klaudisová, M., Schellberg, J., & Honsová, D. (2007). The Rengen grassland experiment: Plant species composition after 64 years of fertilizer application. *Agriculture, Ecosystem & Environment*, *122*, 259–266. https://doi.org/10.1016/j.agee.2006.12.036

Helm, A., Hanski, I., & Pärtel, M. (2006). Slow response of plant species richness to habitat loss and fragmentation. *Ecology Letters*, *9*, 72–77. https://doi.org/10.1111/j.1461-0248.2005.00841.x

Hensgen, F., Bühle, L., & Wachendorf, M. (2016). The effect of harvest, mulching and low-dose fertilization of liquid digestate on above ground biomass yield and diversity of lower mountain semi-natural grasslands. *Agriculture, Ecosystem & Environment*, *216*, 283–292. https://doi.org/10.1016/j.agee.2015.10.009

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E. K., Hungate, B. A., Matulich, K. L., … O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*, 105–108. https://doi.org/10.1038/nature11118

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., … Eisenhauer, N. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, *526*, 574–577. https://doi.org/10.1038/nature15374

Isbell, F., Reich, P. B., Tilman, D., Hobbie, S. E., Polasky, S., & Binder, S. (2013). Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *110*, 11911–11916. https://doi.org/10.1073/pnas.1310880110

Jacquemyn, H., Brys, R., & Hermy, M. (2003). Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biological Conservation*, *111*, 137–147. https://doi.org/10.1016/S0006-3207(02)00256-2

Johansson, L. J., Hall, K., Prentice, H. C., Ihse, M., Reitalu, T., Sykes, M. T., & Kindström, M. (2008). Semi-natural grassland continuity, long-term land-use change and plant species richness in an agricultural landscape on Öland, Sweden. *Landscape and Urban Planning*, *84*, 200–211. https://doi.org/10.1016/j.landurbplan.2007.08.001

Kidd, J., Manning, P., Simkin, J., Peacock, S., & Stockdale, E. (2017). Impacts of 120 years of fertilizer addition on a temperate grassland ecosystem. *PLoS ONE*, *12*, e0174632. https://doi.org/10.1371/journal.pone.0174632

Kleijn, D., Kohler, F., Báldi, A., Batáry, P., Concepción, E. D., Clough, Y., … Verhulst, J. (2009). On the relationship between farmland biodiversity and land-use intensity in Europe. *Proceedings of the Royal Society Biological Sciences*, *276*, 903–909. https://doi.org/10.1098/rspb.2008.1509

Kováčiková, Z., Vargová, V., & Jančová, L. (2013). Effect of digestate application on herbage quality and quantity of permanent grassland. *Agriculture*, *59*, 88–98. https://doi.org/10.2478/agri-2013-0008

Lepš, J. (2014). Scale- and time-dependent effects of fertilization, mowing and dominant removal on a grassland community during a 15-year experiment. *Journal of Applied Ecology*, *51*, 978–987. https://doi.org/10.1111/1365-2664.12255

Liira, J., Ingerpuu, N., Kalamees, R., Moora, M., Pärtel, M., Püssa, K., … Zobel, M. (2012). Grassland diversity under changing productivity and the underlying mechanisms – Results of a 10-yr experiment. *Journal of Vegetation Science*, *23*, 919–930. https://doi.org/10.1111/j.1654-1103.2012.01409.x

Mašková, Z., Doležal, J., Kvet, J., & Zemek, F. (2009). Long-term functioning of a species- rich mountain meadow under different management regimes. *Agriculture, Ecosystem & Environment*, *132*, 192–202. https://doi.org/10.1016/j.agee.2009.04.002

Pärtel, M., Bruun, H. H., & Sammul, M. (2005). Biodiversity in temperate European grasslands: Origin and conservation. In R. Lillak, R. Viiralt,

A. Linke, & V. Geherman (Eds.), *Integrating efficient grassland farming and biodiversity* (pp. 1–14). Tartu: Estonian Grassland Society.

Pärtel, M., Szava-Kovats, R., & Zobel, M. (2011). Dark diversity: Shedding light on absent species. *Trends in Ecology & Evolution*, *26*, 124–128. https://doi.org/10.1016/j.tree.2010.12.004

Pykälä, J., Luoto, M., Heikkinen, R. K., & Kontula, T. (2005). Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic and Applied Ecology*, *6*, 25–33. https://doi.org/10.1016/j.baae.2004.10.002

Sammul, M., Kull, K., & Kattai, K. (2013). Long-time fertilization experiment on Laelatu wooded meadow. *Estonia Maritima*, *9*, 39–79.

Silvertown, J., Poulton, P., Johnston, E., Edwards, G., Heard, M., & Biss, P. M. (2006). The park grass experiment 1856–2006: Its contribution to ecology. *Journal of Ecology*, *94*, 801–814. https://doi.org/10.1111/j.1365-2745.2006.01145.x

Smits, N. A. C., Willems, J. H., & Bobbink, R. (2008). Long-term after-effects of fertilisation on the restoration of calcareous grasslands. *Applied Vegetation Science*, *11*, 279–286. https://doi.org/10.3170/2008-7-18417

Socher, S. A., Prati, D., Boch, S., Müller, J., Baumbach, H., Gockel, S., … Fischer, M. (2013). Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in Germany differ between regions. *Basic and Applied Ecology*, *14*, 126–136. https://doi.org/10.1016/j.baae.2012.12.003

Storkey, J., Macdonald, A. J., Poulton, P. R., Scott, T., Köhler, I. H., Schnyder, H., … Crawley, M. J. (2015). Grassland biodiversity bounces back from long-term nitrogen addition. *Nature*, *528*, 401–404. https://doi.org/10.1038/nature16444

Suding, K. N., Collins, L. S., Gough, L., Clark, C., Cleland, E. E., Gross, L. K., … Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 4387–4392. https://doi.org/10.1073/pnas.0408648102

Tilman, D. (1987). Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, *57*, 190–214. https://doi.org/10.2307/2937080

Tilman, D., Dodd, M. E., Silvertown, J., Poulton, P. R., Johnston, A. E., & Crawley, M. J. (1994). The park grass experiment: Insights from the most long-term ecological study. In R. A. Leigh, & A. E. Johnston (Eds.), *Long-term experiments in agricultural and ecological sciences* (pp. 287–303). Wallingford, UK: CAB International.

Tilman, D., & Isbell, F. (2015). Biodiversity: Recovery as nitrogen declines. *Nature*, *528*, 336–337. https://doi.org/10.1038/nature16320

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and ecosystem functioning. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity-ecosystem service management. *Ecology Letters*, *8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Uchida, K., & Ushimaru, A. (2014). Biodiversity declines due to land abandonment and intensification of agricultural lands: Patterns and mechanisms. *Ecological Monographs*, *84*, 637–658. https://doi.org/10.1890/13-2170.1

Uematsu, Y., & Ushimaru, A. (2013). Topography- and management-mediated resource gradients maintain rare and common plant diversity around paddy terraces. *Ecological Applications*, *23*, 1357–1366. https://doi.org/10.1890/12-1939.1

Van der Hoek, D., Mierlo Anita, J. E. M., & Groenendael, J. M. (2004). Nutrient limitation and nutrient-driven shifts in plant species composition in a species-rich fen meadow. *Journal of Vegetation Science*, *15*, 389–396. https://doi.org/10.1111/j.1654-1103.2004.tb02276.x

Van der Maarel, E., & Sykes, M. T. (1993). Small-scale plant species turnover in a limestone grassland: The carousel model and some comments on the niche concept. *Journal of Vegetation Science*, *4*, 179–188. https://doi.org/10.2307/3236103

Veen, P., Jefferson, R., de Smidt, J., & Van der Straaten, J. (2009). *Grasslands in Europe of high nature value*. Zeist: KNNV Publishing.

Weisser, W. W., Roscher, C., Meyer, S., Ebeling, A., Luo, G., Allan, E., … Eisenhauer, N. (2017). Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. *Basic and Applied Ecology*, *23*, 1–73. https://doi.org/10.1016/j.baae.2017.06.002

Wilson, J. B., Peet, R. K., Dengler, J., & Pärtel, M. (2012). Plant species richness: The world records. *Journal of Vegetation Science*, *23*, 796–802. https://doi.org/10.1111/j.1654-1103.2012.01400.x

Wortley, L., Hero, J.-M., & Howes, M. (2013). Evaluating ecological restoration success: A review of the literature. *Restoration Ecology*, *21*, 537–543. https://doi.org/10.1111/rec.12028

Zhang, P., Zhou, X., Li, J., Guo, Z., & Du, G. (2015). Space resource utilisation: A novel indicator to quantify species competitive ability for light. *Scientific Reports*, *5*, 16832. https://doi.org/10.1038/srep16832

How to cite this article: Melts I, Lanno K, Sammul M, et al. Fertilising semi-natural grasslands may cause long-term negative effects on both biodiversity and ecosystem stability. *J Appl Ecol*. 2018;55:1951–1955. https://doi.org/10.1111/1365-2664.13129