Title: Local nutrient addition drives plant biodiversity losses but not biotic homogenization in global grasslands

Authors:
Qingqing Chen[1,2*], Shane A. Blowes[1,3], W. Stanley Harpole[1,4,5], Emma Ladouceur[1,3], Elizabeth T. Borer[6],Andrew MacDougall[7], Jason P. Martina[8], Jonathan D. Bakker9[9], Pedro M. Tognetti[10,11], Eric W. Seabloom[6], Pedro Daleo[12], Sally Power[13], Christiane Roscher[1,4], Peter Adler[14], Ian Donohue[15], George Wheeler[16], Carly Stevens[17], Ciska Veen[18], Anita C. Risch[11], Glenda M. Wardle[19], Yann Hautier[20], Catalina Estrada[21], Erika Hersch-Green[22], Yujie Niu[23], Pablo L. Peri[24], Anu Eskelinen[1,4,25], Daniel S Gruner[26], Harry Olde Venterink[27], Carla D'Antonio[28], Marc W. Cadotte[29], Sylvia Haider[1,30], Nico Eisenhauer[1,31], Jane Catford[32,33], Risto Virtanen[25], John W. Morgan[34], Michelle Tedder[35], Sumanta Bagchi[36], Maria C. Caldeira[37], Miguel Bugalho[38], Johannes M. H. Knops[39], Chris R. Dickman[40], Nicole Hagenah[41], Anke Jentsch[23], Petr Macek[42], Brooke B. Osborne[43], Lauri Laanisto[44] , Jonathan M. Chase[1,3]

Affiliations:

1. German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig.
2. Senckenberg Museum for Natural History Görlitz, D-02826, Görlitz, Germany.
3. Department of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany.
4. Helmholtz Center for Environmental Research – UFZ, Department of Physiological Diversity, Permoserstrasse 15, 04318 Leipzig, Germany.
5. Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle (Saale), Germany.
6. Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108 USA.
7. Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G2W1.
8. Department of Biology, Texas State University, San Marcos, TX, 78666 USA.
9. School of Environmental and Forest Sciences, University of Washington, Seattle, WA USA.
10. Instituto de Investigaciones Fisiológicas y Ecológicas Vinculadas a La Agricultura (IFEVA), Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Buenos Aires, Argentina.
11. Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland.
12. Instituto de Investigaciones Marinas y Costeras (IIMyC), UNMdP-CONICET, CC 1260 Correo Central, Mar Del Plata B7600WAG, Argentina.
13. Hawkesbury Institute for Hte Environment, Locked Bag 1797, Penrith, New South Wales, 2751, Australia.
14. Department of Wildland Resources and the Ecology Center, Utah State University, Logan, UT, 84322 USA.
15. Zoology, School of Natural Sciences, Trinity College Dublin, Dublin, Ireland.
16. University of Nebraska-Lincoln, Lincoln, NE, USA.
17. Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK.
18. Department of Terrestrial Ecology, Netherlands Institute of Ecology, Droevedaalsesteeg 10, 6708 PB, Wageningen, The Netherlands.
19. Desert Ecology Research Group, School of Life and Environmental Sciences, ARC Training Centre in Data Analytics for Resources and Environments (DARE), The University of Sydney, NSW 2006, Australia.
20. Ecology and Biodiversity Group, Department of Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands.

21. Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK.
22. Department of Biological Sciences, Michigan Technological University, Houghton, MI 49930, USA.
23. Disturbance Ecology and Vegetation Dynamics, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Germany.
24. Instituto Nacional de Tecnología Agropecuaria (INTA), Universidad Nacional de La Patagonia Austral (UNPA).CONICET. Río Gallegos, Santa Cruz, Argentina.
25. Ecology & Genetics Unit, University of Oulu, Finland.
26. Department of Entomology, University of Maryland, College Park, MD USA.
27. Vrije Universiteit Brussel, Department Biology, WILD, Pleinlaan 2, 1050 Brussels, BELGIUM.
28. Dept. of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada.
29. University of California, Santa Barbara.
30. Institute of Ecology, Leuphana University of Lüneburg, Universitätsallee 1, 21335 Lüneburg, Germany.
31. Institute of Biology, Leipzig University; Puschstrasse 4, 04103 Leipzig, Germany.
32. Department of Geography, King's College London, 30 Aldwych, London, WC2B 4BG, UK.
33. School of Ecosystem & Forest Sciences, University of Melbourne, Parkville, VIC 3010, Australia.
34. Department of Environment & Genetics, La Trobe University, Bundoora 3083, Victoria, Australia.
35. Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
36. Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India.
37. Forest Research Centre, Associate Laboratory TERRA, School of Agriculture, University of Lisbon, Portugal.
38. Centre for Applied Ecology 'Prof. Baeta Neves' (CEABN-InBIO), School of Agriculture, University of Lisbon, Portugal.
39. Health & Environmnetal Sciences Department, Xi'an Jiaoting-Liverpool University, Suzhou, Jiangsu, China.
40. Desert Ecology Research Group, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
41. Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa.
35. Centre for Functional Biodiversity, School of Life Sciences, University of KwaZulu-Natal, Pietermaritzburg, South Africa.
36. Centre for Ecological Sciences, Indian Institute of Science, Bangalore, India.
37. Forest Research Centre, Associate Laboratory TERRA, School of Agriculture, University of Lisbon, Portugal.
38. Centre for Applied Ecology 'Prof. Baeta Neves' (CEABN-InBIO), School of Agriculture, University of Lisbon, Portugal.
39. Health & Environmnetal Sciences Department, Xi'an Jiaoting-Liverpool University, Suzhou, Jiangsu, China.
40. Desert Ecology Research Group, School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia.
41. Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa.
42. Institute of Hydrobiology, Biology Centre of the Czech Academy of Sciences, Na Sadkach 7, Ceske Budejovice 370 05, Czech Republic

43. Department of Environment and Society, Utah State University, Moab, UT, USA
44. Chair of Biodiversity and Nature Tourism, Estonian University of Life Sciences, Kreutzwaldi 5, 51006, Tartu, Estonia

*corresponding author: chqq365@gmail.com

Abstract:

Nutrient enrichment typically causes local plant biodiversity decline due to losses of rare species and species with traits ill-suited for high nutrient levels. These local-scale losses can cause biotic homogenization at larger scales if they outpace losses of widespread species. This is a common, but untested, expectation. Using a standardized experiment across 72 grasslands on six continents, we found similar magnitudes of losses of spatially restricted and widespread species, causing proportional species loss at local and larger scales and no biotic homogenization, even up to 14 years of treatment. Such patterns of diversity changes held consistent across plant origins and life form variations. Thus, nutrient enrichment poses threats to all functional groups including dominant widespread species that are often critical for ecosystem functions and services.

One-Sentence Summary:

No evidence for biotic homogenization following fertilization in grasslands worldwide

Main Text:
Agricultural fertilization practices and atmospheric nutrient deposition have led to increased availability and redistribution of soil nutrients globally (*1–3*). At local scales, nutrient enrichment tends to reduce plant biodiversity (i.e. α diversity) (*4*, *5*). This biodiversity decline is typically ascribed to disproportionate losses of rare species (i.e. species with low abundance), and/or the removal of species with particular traits ill-suited for effectively competing in high nutrient conditions (*6*). Rare species can be lost or displaced regardless of their traits (*6–8*) because small populations are more susceptible to extinction. Spatially restricted species (hereafter referred to as localized species) are often rare (*9*), and tend to have narrow environmental tolerances, and are thus less likely to persist with changes in nutrient levels (*10*). While species can vary widely in their nutrient requirements and tolerances, groups of species with similar (shared) characteristics such as plant origins and life forms can be lost from a flora. For example, native species are more likely to be lost than non-native species when nutrients are enriched because non-natives are often better-adapted to nutrient-rich conditions (*6*, *11*, *12*). Similarly, legumes may be lost more than non-legume species in high nutrient environments due to decreased competitive advantage of nitrogen-fixing species (*6*, *13*).

Despite clear evidence that nutrient enrichment causes losses of α diversity in grasslands (*4*, *5*), how these losses scale up to larger spatial scales (i.e. γ diversity; calculated by aggregating local communities) is less straightforward (*14–16*). Yet, it is biodiversity loss and change at larger scales that are most often relevant for biodiversity conservation and management, as well as for its role in ecosystem functions and services (*17*). It is often assumed that nutrient enrichment, like many other global changes, results in biotic homogenization (i.e. less variation in species composition among local communities, frequently quantified as a decrease in β diversity) (*18–21*). Specifically, high levels of nutrient addition is expected to homogenize soil nutrients, and create conditions that consistently select for a few species that are nutrient-demanding, fast-growing, and highly competitive for light (*22*, *23*). Indeed, nutrient-demanding and faster-growing species tend to be more widespread than species with lower nutrient requirements because they produce smaller seeds, which enable them to disperse more widely (*24*, *25*). While some experimental studies support the notion that nutrient enrichment leads to homogenization (*26–28*), other studies have found no changes in β diversity (*29–32*) or even differentiation (i.e. increase in β diversity) (*33–39*). More importantly, clear links between nutrient enrichment and changes in the numbers of localized versus widespread species, and the subsequent changes in β diversity are yet to be made.

We can more explicitly investigate the scale-dependent nature of biodiversity change in response to nutrient enrichment by quantifying change in alpha ($\Delta\alpha$), gamma ($\Delta\gamma$), and beta ($\Delta\beta$) diversity simultaneously. A recent extension to Whittaker's multiplicative β diversity partition (i.e. $\Delta\beta = \Delta\gamma/\Delta\alpha$) shows how investigating $\Delta\alpha$, $\Delta\gamma$, and $\Delta\beta$ can be linked to changes in the numbers of localized and widespread species (Fig. 1A) (*14*, *40*). This framework shows that nutrient enrichment could cause vegetation homogenization if local communities gain widespread species (scenario I in Fig. 1A), or if localized species are replaced by widespread species (scenario II in Fig.1A), or if the numbers of localized species decreases (scenario III in Fig. 1A). Conversely, nutrient enrichment could cause vegetation differentiation if local communities lose widespread

species (scenario IV in Fig. 1A), or if widespread species are replaced by localized species (scenario V in Fig.1A), or if the number of localized species increases (scenario VI in Fig.1A). The framework also shows that if gains or losses of species at the α and γ scale are similar, then we would observe no change in β diversity (1:1 diagonal line in Fig. 1A). The species losses at local scales following nutrient addition suggests that if nutrient enrichment is to cause vegetation homogenization it is most likely associated with losses of localized species outpacing that of widespread species, resulting in $\Delta\gamma < \Delta\alpha$ (Fig. 1B to Fig. 1C). However, if losses of localized and widespread species at similar magnitudes, resulting in $\Delta\gamma \approx \Delta\alpha$, nutrient enrichment could lead to no change in β diversity (Fig. 1B to Fig. 1D). Alternatively, nutrient enrichment can be associated with the loss of widespread species, resulting in $\Delta\gamma > \Delta\alpha$ and causing vegetation differentiation (Fig. 1B to Fig.1E). In this study, we use this framework to synthesize scale-dependent plant biodiversity change in response to nutrient enrichment from a long-term standardized nutrient addition experiment distributed across 72 grasslands on six continents (i.e. NutNet; Fig. S1 and Table S1; ref (*41*)).

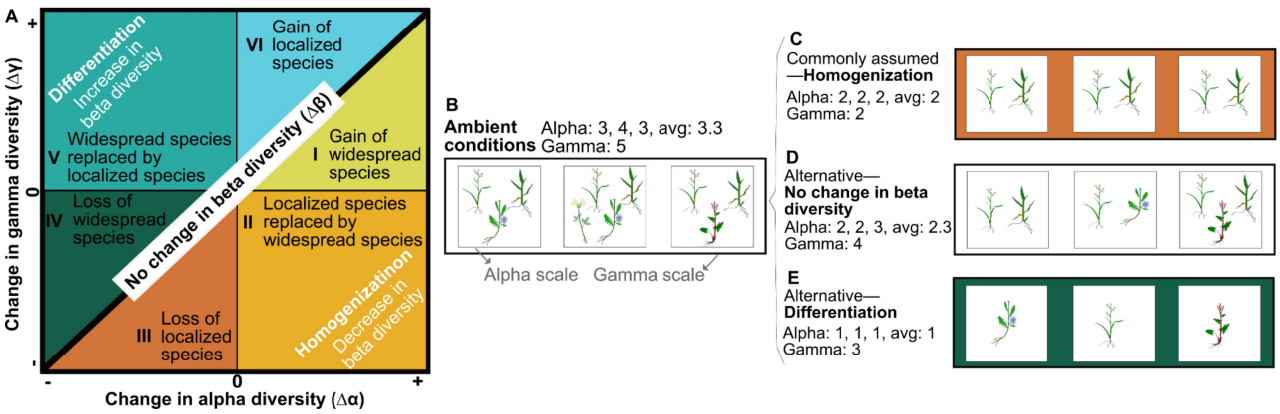

Fig 1. Conceptual framework linking biodiversity changes at the alpha-, gamma-, and beta-scales, and alternative hypotheses for how nutrient enrichment affects plant biodiversity at each scale. **(A)** An integrated framework to understand biodiversity change under anthropogenic drivers across spatial scales through change in localized and widespread species. Adapted from (*14*). Δα, Δγ, and Δβ are changes in alpha, gamma and beta diversity under anthropogenic drivers such as nutrient enrichment. Δβ is separated by the 1:1 diagonal line. Above the diagonal line, $\Delta\gamma > \Delta\alpha$, $\Delta\beta > 0$, nutrient enrichment causes vegetation differentiation. Below the diagonal line, $\Delta\gamma < \Delta\alpha$, $\Delta\beta < 0$, nutrient enrichment causes vegetation homogenization. Moreover, homogenization can be attributed to three scenarios including I: gain of widespread species ($\Delta\gamma < \Delta\alpha$, and $\Delta\gamma > 0$, $\Delta\alpha > 0$); II: Localized species replaced by widespread species ($\Delta\gamma < \Delta\alpha$, $\Delta\gamma < 0$ and $\Delta\alpha > 0$); III: Loss of localized species ($\Delta\gamma < \Delta\alpha$, and $\Delta\gamma < 0$, $\Delta\alpha < 0$). Conversely, differentiation can be attributed to three scenarios that include IV: Loss of widespread species ($\Delta\gamma > \Delta\alpha$, and $\Delta\gamma < 0$, $\Delta\alpha < 0$); V: Widespread species replaced by localized species ($\Delta\gamma > \Delta\alpha$, $\Delta\gamma > 0$ and $\Delta\alpha < 0$); VI: gain of localized species ($\Delta\gamma > \Delta\alpha$, and $\Delta\gamma > 0$, $\Delta\alpha > 0$). **(B-E)** potential effects of nutrient enrichment on plant biodiversity across spatial scales. Nutrient enrichment most likely cause vegetation homogenization through loss of localized species (scenario III; see text for explanations). Alternatively, nutrient addition can cause no change in Δβ if loss of localized and widespread species at the same magnitude (the diagonal line) or vegetation differentiation through loss of

widespread species (IV).

We investigated plant biodiversity changes under nutrient addition by nitrogen, phosphorus, and potassium relative to ambient conditions within sites. Nutrients were added to 5 m × 5 m plots in 3 blocks at each site at a rate of 10 g m^{-2} y^{-1}. We focused on species richness for this analysis, because it is the most commonly examined plant diversity metric (*42*). At each site, α diversity was the average number of species over 3 blocks for each treatment, γ diversity was calculated as the total number of species occurring over 3 blocks for each treatment. We estimated Δα and Δγ 4 years after adding nutrients, and then used this to estimate Δβ (Whittaker's β diversity on the log scale; Fig. 2; see model fit in Fig. S2 and Table S2). Overall, adding nutrients decreased α and γ diversity, but it had no significant effects on β diversity (Fig. 2; Table S3), see also (*30*). This means that losses of localized and widespread species were of a similar magnitude. At the site level, there was substantial variation in Δγ, and to a less extent Δα, little variation in Δβ (Fig. S3; also see Table S4 for site-level estimate). While it is possible that drought intensity, grazing intensity, site productivity, and/or site species pool (*29*, *33*, *35*, *43*) could mediate the response of α, γ, and β to nutrient addition, we failed to detect any strong correlation with these site covariates (Fig. S4). Larger-scale processes (e.g., biotic interactions from herbivores or pollinators) are unlikely to be affected by the scale of our nutrient addition. It is thus possible that larger-scale (e.g. landscape) nutrient addition experiments may affect these populations differently, leading to feedback on the plants. Importantly, the effects of nutrient addition on α, γ, and β diversity when we used metrics accounting for species abundance (e.g. Shannon diversity and Simpson diversity) were consistent with that of species richness (Fig. S5; Table S3). This suggests that nutrient addition decreased rare and abundant species by similar magnitudes. Taken together, our results suggest that plant biodiversity declines across spatial scales under nutrient addition were independent of species abundances and of species range distribution (i.e. localized or widespread species).

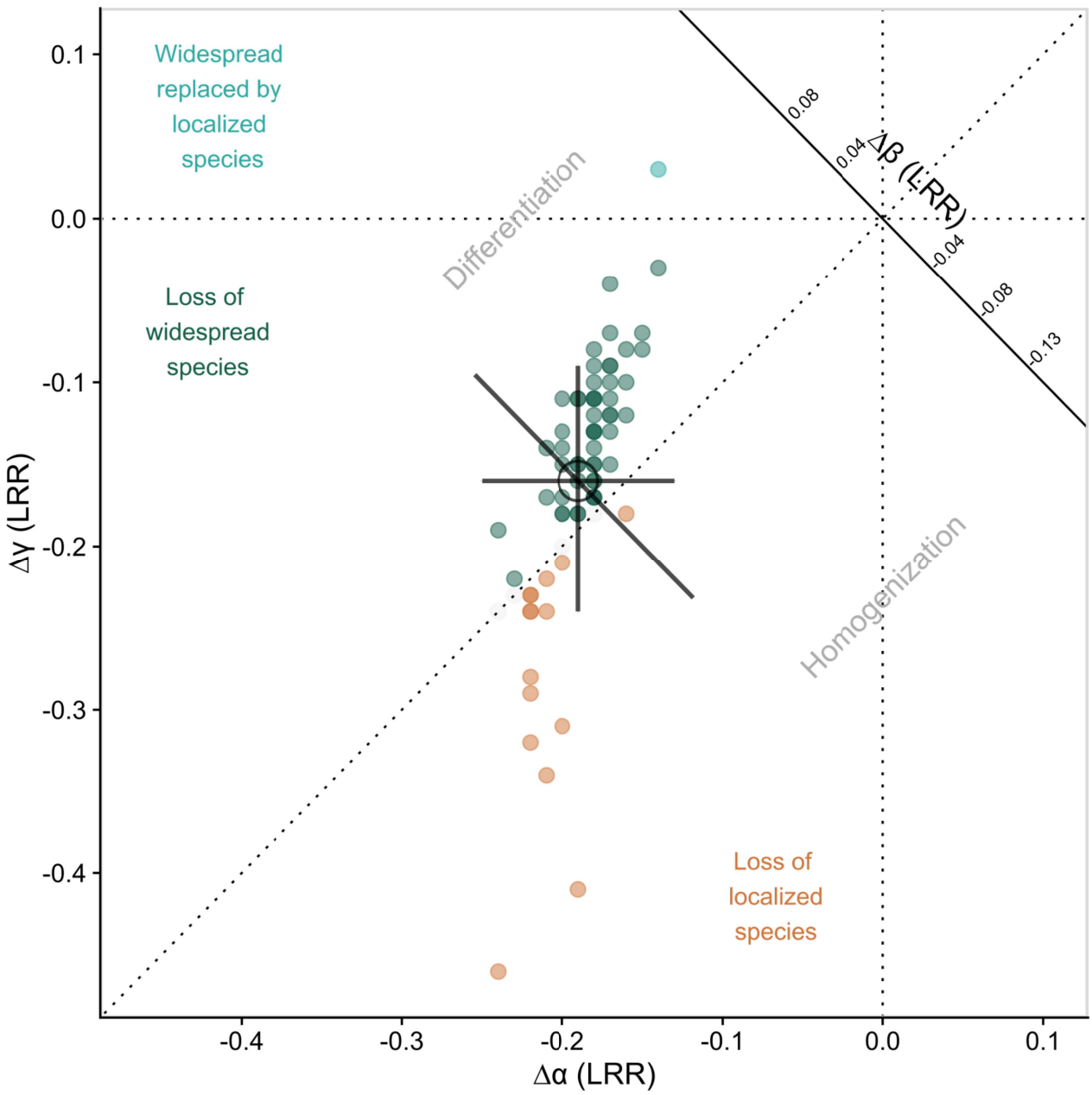

Fig. 2. Effects of nutrient addition on alpha, gamma, and beta diversity (Δα, Δγ, and Δβ). Δα and Δγ are the estimated diversity changes 4 years after nutrient addition compared with the ambient conditions on the log scale (i.e. LRR; log response ratio). Δβ is calculated as (Δγ - Δα; i.e. Whittaker's beta diversity on the log scale). Horizontal, vertical, and diagonal dotted lines indicate no effects of nutrient addition on γ, α, and β diversity respectively; the solid diagonal line shows the axis and scale for Δβ. Colors for small points correspond to scenarios of changes in widespread and localized species shown in Fig. 1A (i.e., six sections divided by the three dotted lines with scenarios indicated in text). The large open point and thick error bars are the overall effects of nutrient addition on α, γ, and β diversity. Error bars are 95% confidence intervals. See Table S2 for model specification and fit. See Table S3 for estimated overall means and 95% confidence intervals of Δα, Δγ, and Δβ. See Fig. S3 and Table S4 for site-level estimates and 95% confidence intervals.

To check whether patterns of plant biodiversity changes across spatial scales under nutrient addition

held consistent across groups of species with similar characteristics, we investigate changes in α, γ, and β diversity within groups of plant origins and life forms. Extending previous studies (*6*, *44*), we found that nutrient addition not only caused reduction of α diversity, but also γ diversity, of native plants much more than that of non-native species (Fig. 3; Table S5; Table S6). For instance, nutrient addition decreased γ diversity of native species three times more than that of non-native species (effects on non-native species were not statistically significant; Table S6). Nutrient addition decreased α and γ diversity to similar magnitudes in native species (Fig. 3A; Fig. S6). It decreased α diversity much stronger than γ diversity in non-native species (Fig. 3B; Fig. S6). Meanwhile we observed more site-level variations in α and γ diversity in non-native than native species (Fig. 3B; Fig. S6). For instance, non-native species even gained localized or widespread species at some sites (Fig. 3B). As a result, nutrient addition did not affect β diversity within groups of native or non-native species. This contrasts with a previous study suggesting that non-native species naturalization, rather than native species diversity loss, causes biotic homogenization (*18*) However, the scale of that study was at much more broader geographic scales, while ours focused on within-site patterns. To determine whether scale-dependent biodiversity changes varied among life forms we divided the species into forbs, woody, graminoid and legume species. We found that nutrient addition led to the greatest reduction of α diversity in forb species, followed by woody, graminoid, and legume species (effects on legume species were not statistically significant; Fig. 4; Table S7; Table S8). We observed stronger site-level variation in the responses of legumes species to nutrient addition with α diversity decline > 67% at some sites (Fig. 4C; Fig. S7). However, nutrient addition only led to the reduction of γ diversity in graminoids (effects on the other three life forms were not statistically significant; Fig. 4; Table S7). We also observed more site-level variations in γ diverstiy for forb and woody species that that of graminoid species (Fig. 4; Fig. S7). These results contrast to expectations that legumes are more likely to be lost than other life forms under nitrogen addition (*6*). This is probably because legume species are often negatively affected by nitrogen addition, but they could be promoted by the phosphorus addition (*13*), thus, adding nitrogen, phosphorus, and potassium together as in our experiment may cause weaker responses of legume species. Importantly, nutrient addition decreased α and γ diversity to a similar magnitude for graminoids, legumes, and woody species (Fig. 4; Table S8). It decreased α diversity much stronger than γ diversity for forb species, but meanwhile site-level Δr varied more widely than Δα (Fig. 4B; Table S8). Overall, nutrient addition did not cause vegetation homogenization or differentiation for any of these species groups due to losses of localized and widespread species at similar magnitudes.

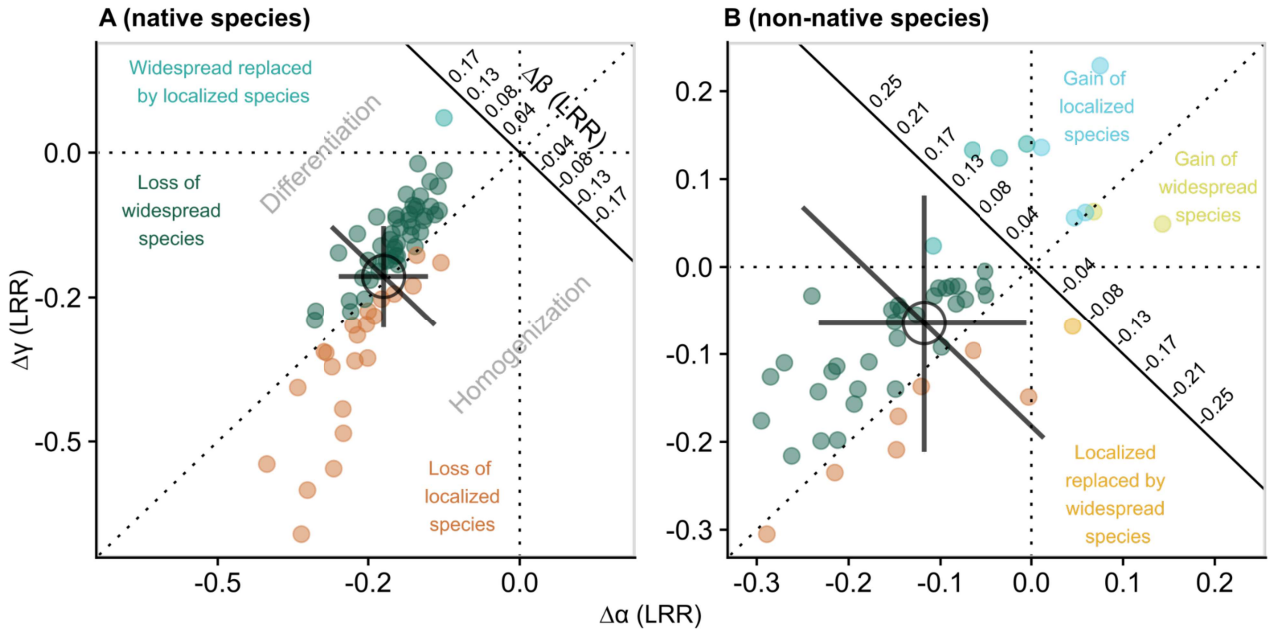

Fig. 3. Effects of nutrient addition on alpha, gamma, and beta diversity (Δα, Δγ, and Δβ) for (A) native and (B) non-native species. Δα and Δγ are the estimated diversity changes 4 years after nutrient addition compared with the ambient conditions on the log scale (i.e. LRR; log response ratio). Δβ is calculated as (Δγ - Δα; i.e. Whittaker's beta diversity on the log scale). Horizontal, vertical, and diagonal dotted lines indicate no effects of nutrient addition on γ, α, and β diversity respectively; the solid diagonal line shows the axis and scale for Δβ. Colors for small points correspond to scenarios of changes in widespread and localized species shown in Fig. 1A (i.e., six sections divided by the three dotted lines with scenarios indicated in text). The large open point and thick error bars are the overall effects of nutrient addition on α, γ, and β diversity. Error bars are 95% confidence intervals. See Table S5 for model specification and fit. See Table S6 for estimated overall means and 95% confidence intervals for Δα, Δγ, and Δβ for native and non-native species. See Fig. S6 for 95% confidence intervals at site level.

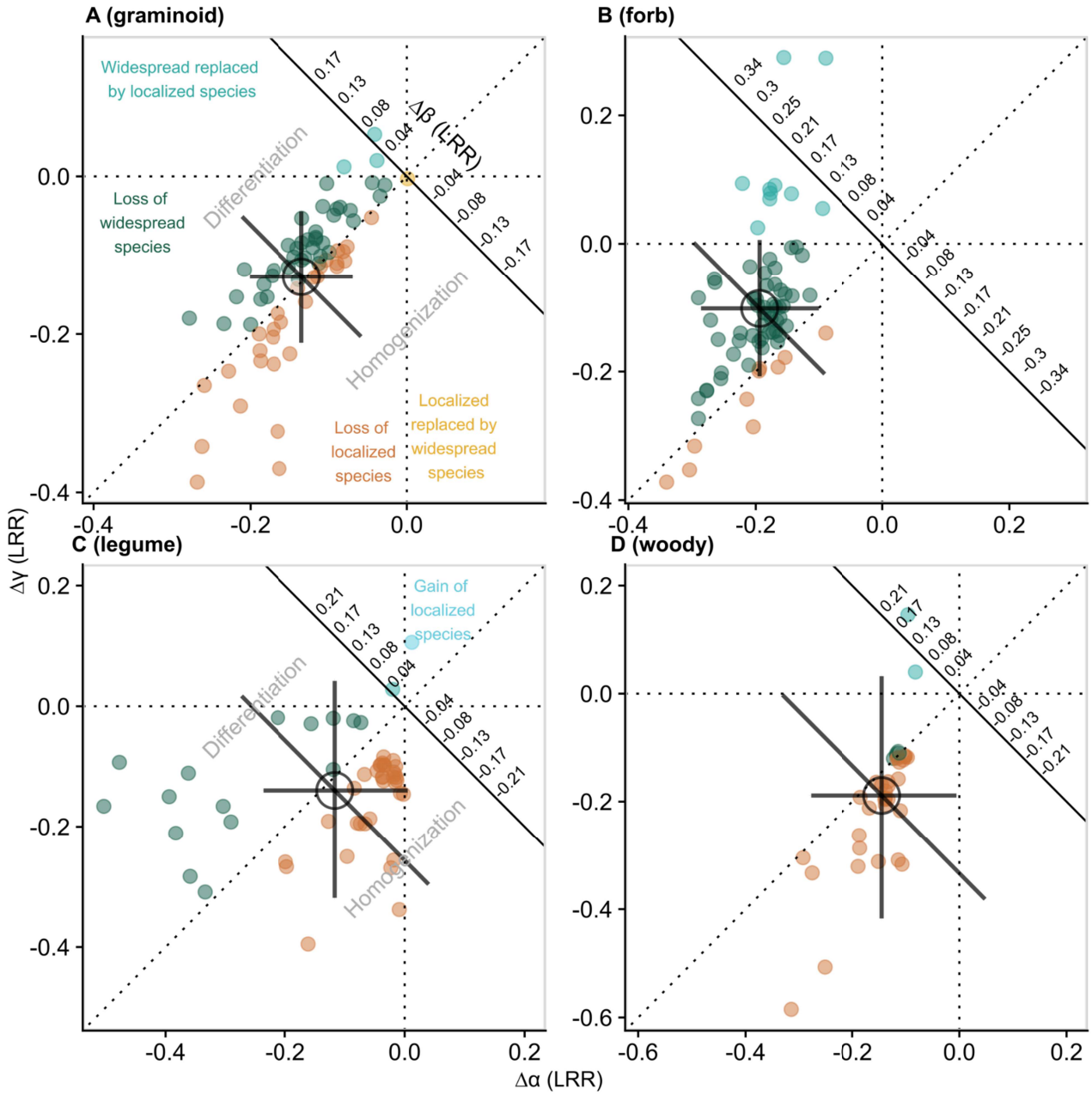

Fig. 4. Effects of nutrient addition on alpha, gamma, and beta diversity (Δα, Δγ, and Δβ) for (A) graminoid, (B) forb, (C) legume, and (D) woody species. Δ*α* and Δγ are the estimated diversity changes 4 years after nutrient addition compared with the ambient conditions on the log scale (i.e. LRR; log response ratio). Δβ is calculated as (Δγ - Δα; i.e. Whittaker's beta diversity on the log scale). Horizontal, vertical, and diagonal dotted lines indicate no effects of nutrient addition on γ, α, and β diversity respectively; the solid diagonal line shows the axis and scale for Δβ. Colors for small points correspond to scenarios of changes in widespread and localized species shown in Fig. 1A (i.e., six sections divided by the three dotted lines with scenarios indicated in text). The large open point and thick error bars are the overall effects of nutrient addition on α, γ, and β diversity. Error bars are 95% confidence intervals. See Table S7 for model specification and fit. See Table S8 for estimated overall means and 95% confidence intervals for Δ*α*, Δ*γ,* and Δβ for forb, graminoid, legume, and woody species. See Fig. S7 for 95% confidence intervals at site level.

We tested the robustness of our results by performing multiple sensitivity tests, including using longer-term time series, and a subset of data with greater within-site replication. Previous single-site experiments show that nutrient addition may cause vegetation homogenization in the longer term (>3 years) but not short term (*26*, *28*). To examine whether experimental duration influenced our results, we redid analyses using data from 29 sites that had 10 years of nutrient addition (Fig. S8 ~ Fig. S11), and again using data from 16 sites with 14 years of nutrient addition (Fig. S12 ~ Fig. S15). These analyses included 1) the effects of nutrient addition on *α,* γ, and β diversity, 2) the relationships between these diversity changes and site covairates, 3) diversity changes within groups of plant origins, 4) diversity changes within groups of life forms. The overall effects were similar to that of four years of nutrient addition. Moreover, because combining three blocks to create our γ scale encompassed a limited spatial extent, we tested whether combining more blocks to create the γ scale altered our results. To do this, we redid the analyses using data from 16 sites that had four spatial blocks (Fig. S16~Fig. S19), and again using data from 11 sites that had five spatial blocks (Fig. S20 ~ Fig. S23). Again, the overall effects were similar to that of 72 sites with three blocks that we presented above.

In total, we provide a comprehensive synthesis of the impact of nutrient addition on scale-dependent plant biodiversity change from a standardized long-term experiment in grasslands worldwide. We found overall proportional plant biodiversity declines at local and larger spatial scales under nutrient addition, thus no vegetation homogenization within sites. This is due to losses of localized and widespread species at similar magnitudes following nutrient addition. Such patterns of diversity change also held consistent across plant origins and life forms as well as over longer time periods (10 and 14 years' treatment). These results demonstrate that nutrient enrichment poses a potential threat to all functional groups including widespread dominant species that often determine ecosystem functions and services.

References and notes:

1. J. Sardans, J. Peñuelas, Potassium: a neglected nutrient in global change. *Global Ecology and Biogeography* **24**, 261–275 (2015).

2. J. N. Galloway, A. Bleeker, J. W. Erisman, The Human Creation and Use of Reactive Nitrogen: A Global and Regional Perspective. *Annual Review of Environment and Resources* **46**, 255–288 (2021).

3. Z. Yuan, S. Jiang, H. Sheng, X. Liu, H. Hua, X. Liu, Y. Zhang, Human Perturbation of the Global Phosphorus Cycle: Changes and Consequences. *Environ. Sci. Technol.* **52**, 2438–2450 (2018).

4. R. Bobbink, K. Hicks, J. Galloway, T. Spranger, R. Alkemade, M. Ashmore, M. Bustamante, S. Cinderby, E. Davidson, F. Dentener, B. Emmett, J. W. Erisman, M. Fenn, F. Gilliam, A. Nordin, L. Pardo, W. De Vries, Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications* **20**, 30–59 (2010).

5. E. W. Seabloom, P. B. Adler, J. Alberti, L. Biederman, Y. M. Buckley, M. W. Cadotte, S. L. Collins, L. Dee, P. A. Fay, J. Firn, N. Hagenah, W. S. Harpole, Y. Hautier, A. Hector, S. E. Hobbie, F. Isbell, J. M. H. Knops, K. J. Komatsu, R. Laungani, A. MacDougall, R. L. McCulley, J. L. Moore, J. W. Morgan, T. Ohlert, S. M. Prober, A. C. Risch, M. Schuetz, C. J.

Stevens, E. T. Borer, Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecology* **102**, 1–11 (2021).

6. K. N. Suding, S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, S. Pennings, 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 (2005).

7. Z. Yang, Y. Hautier, E. T. Borer, C. Zhang, G. Du, Abundance- and functional-based mechanisms of plant diversity loss with fertilization in the presence and absence of herbivores. *Oecologia* **179**, 261–270 (2015).

8. P. Zhang, E. T. Borer, E. W. Seabloom, M. B. Soons, M. M. Hefting, G. A. Kowalchuk, P. B. Adler, C. Chu, X. Zhou, C. S. Brown, Z. Guo, X. Zhou, Z. Zhao, G. Du, Y. Hautier, Space resource utilization of dominant species integrates abundance- and functional-based processes for better predictions of plant diversity dynamics. *Oikos* **2023**, e09519 (2023).

9. K. J. Gaston, T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, J. H. Lawton, Abundance–occupancy relationships. *Journal of Applied Ecology* **37**, 39–59 (2000).

10. S. Kambach, J. Lenoir, G. Decocq, E. Welk, G. Seidler, S. Dullinger, J.-C. Gégout, A. Guisan, H. Pauli, J.-C. Svenning, P. Vittoz, T. Wohlgemuth, N. E. Zimmermann, H. Bruelheide, Of niches and distributions: range size increases with niche breadth both globally and regionally but regional estimates poorly relate to global estimates. *Ecography* **42**, 467–477 (2019).

11. A. S. MacDougall, J. L. McCune, O. Eriksson, S. A. O. Cousins, M. Pärtel, J. Firn, J. L. Hierro, The Neolithic Plant Invasion Hypothesis: the role of preadaptation and disturbance in grassland invasion. *New Phytologist* **220**, 94–103 (2018).

12. E. W. Seabloom, E. T. Borer, Y. M. Buckley, E. E. Cleland, K. F. Davies, J. Firn, W. S. Harpole, Y. Hautier, E. M. Lind, A. S. Macdougall, J. L. Orrock, S. M. Prober, P. B. Adler, T. M. Anderson, J. D. Bakker, L. A. Biederman, D. M. Blumenthal, C. S. Brown, L. A. Brudvig, M. Cadotte, C. Chu, K. L. Cottingham, M. J. Crawley, E. I. Damschen, C. M. Dantonio, N. M. Decrappeo, G. Du, P. A. Fay, P. Frater, D. S. Gruner, N. Hagenah, A. Hector, H. Hillebrand, K. S. Hofmockel, H. C. Humphries, V. L. Jin, A. Kay, K. P. Kirkman, J. A. Klein, J. M. H. Knops, K. J. La Pierre, L. Ladwig, J. G. Lambrinos, Q. Li, W. Li, R. Marushia, R. L. Mcculley, B. A. Melbourne, C. E. Mitchell, J. L. Moore, J. Morgan, B. Mortensen, L. R. O'halloran, D. A. Pyke, A. C. Risch, M. Sankaran, M. Schuetz, A. Simonsen, M. D. Smith, C. J. Stevens, L. Sullivan, E. Wolkovich, P. D. Wragg, J. Wright, L. Yang, Plant species origin predicts dominance and response to nutrient enrichment and herbivores in global grasslands. *Nature Communications* **6** (2015).

13. P. M. Tognetti, S. M. Prober, S. Báez, E. J. Chaneton, J. Firn, A. C. Risch, M. Schuetz, A. K. Simonsen, L. Yahdjian, E. T. Borer, E. W. Seabloom, C. A. Arnillas, J. D. Bakker, C. S. Brown, M. W. Cadotte, M. C. Caldeira, P. Daleo, J. M. Dwyer, P. A. Fay, L. A. Gherardi, N. Hagenah, Y. Hautier, K. J. Komatsu, R. L. McCulley, J. N. Price, R. J. Standish, C. J. Stevens, P. D. Wragg, M. Sankaran, Negative effects of nitrogen override positive effects of phosphorus on grassland legumes worldwide. *Proceedings of the National Academy of Sciences* **118** (2021).

14. S. A. Blowes, B. McGill, V. Brambilla, C. F. Y. Chow, T. Engel, A. Fontrodona-Eslava, I. S. Martins, D. McGlinn, F. Moyes, A. Sagouis, H. Shimadzu, R. van Klink, W.-B. Xu, N. J.

Gotelli, A. Magurran, M. Dornelas, J. M. Chase, Synthesis reveals approximately balanced biotic differentiation and homogenization. *Science Advances* **10**, eadj9395 (2024).

15. P. Keil, H. M. Pereira, J. S. Cabral, J. M. Chase, F. May, I. S. Martins, M. Winter, Spatial scaling of extinction rates: Theory and data reveal nonlinearity and a major upscaling and downscaling challenge. *Global Ecology and Biogeography* **27**, 2–13 (2018).

16. J. M. Chase, B. J. McGill, P. L. Thompson, L. H. Antão, A. E. Bates, S. A. Blowes, M. Dornelas, A. Gonzalez, A. E. Magurran, S. R. Supp, M. Winter, A. D. Bjorkman, H. Bruelheide, J. E. K. Byrnes, J. S. Cabral, R. Elahi, C. Gomez, H. M. Guzman, F. Isbell, I. H. Myers-Smith, H. P. Jones, J. Hines, M. Vellend, C. Waldock, M. O'Connor, Species richness change across spatial scales. *Oikos* **128**, 1079–1091 (2019).

17. P. Daleo, J. Alberti, E. J. Chaneton, O. Iribarne, P. M. Tognetti, J. D. Bakker, E. T. Borer, M. Bruschetti, A. S. MacDougall, J. Pascual, M. Sankaran, E. W. Seabloom, S. Wang, S. Bagchi, L. A. Brudvig, J. A. Catford, C. R. Dickman, T. L. Dickson, I. Donohue, N. Eisenhauer, D. S. Gruner, S. Haider, A. Jentsch, J. M. H. Knops, Y. Lekberg, R. L. McCulley, J. L. Moore, B. Mortensen, T. Ohlert, M. Pärtel, P. L. Peri, S. A. Power, A. C. Risch, C. Rocca, N. G. Smith, C. Stevens, R. Tamme, G. F. (Ciska) Veen, P. A. Wilfahrt, Y. Hautier, Environmental heterogeneity modulates the effect of plant diversity on the spatial variability of grassland biomass. *Nat Commun* **14**, 1809 (2023).

18. B. H. Daru, T. J. Davies, C. G. Willis, E. K. Meineke, A. Ronk, M. Zobel, M. Pärtel, A. Antonelli, C. C. Davis, Widespread homogenization of plant communities in the Anthropocene. *Nat Commun* **12**, 6983 (2021).

19. M. M. Gossner, T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, S. C. Renner, J. Sikorski, T. Wubet, H. Arndt, V. Baumgartner, S. Blaser, N. Blüthgen, C. Börschig, F. Buscot, T. Diekötter, L. R. Jorge, K. Jung, A. C. Keyel, A.-M. Klein, S. Klemmer, J. Krauss, M. Lange, J. Müller, J. Overmann, E. Pašalić, C. Penone, D. J. Perović, O. Purschke, P. Schall, S. A. Socher, I. Sonnemann, M. Tschapka, T. Tscharntke, M. Türke, P. C. Venter, C. N. Weiner, M. Werner, V. Wolters, S. Wurst, C. Westphal, M. Fischer, W. W. Weisser, E. Allan, Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* **540**, 266–269 (2016).

20. I. R. Staude, D. M. Waller, M. Bernhardt-Römermann, A. D. Bjorkman, J. Brunet, P. De Frenne, R. Hédl, U. Jandt, J. Lenoir, F. Máliš, K. Verheyen, M. Wulf, H. M. Pereira, P. Vangansbeke, A. Ortmann-Ajkai, R. Pielech, I. Berki, M. Chudomelová, G. Decocq, T. Dirnböck, T. Durak, T. Heinken, B. Jaroszewicz, M. Kopecký, M. Macek, M. Malicki, T. Naaf, T. A. Nagel, P. Petřík, K. Reczyńska, F. H. Schei, W. Schmidt, T. Standovár, K. Świerkosz, B. Teleki, H. Van Calster, O. Vild, L. Baeten, Disentangling non-random structure from random placement when estimating β-diversity 1 through space or time. *Nat Ecol Evol* **4**, 802–808 (2020).

21. M. L. McKinney, J. L. Lockwood, Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* **14**, 450–453 (1999).

22. M. Huston, A General Hypothesis of Species Diversity. *The American Naturalist* **113**, 81–101 (1979).

23. *Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton University Press, Princeton, New Jersey, USA.*

24. J. P. Grime, Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. *The American Naturalist* **111**, 1169–1194 (1977).

25. J. Sonkoly, B. Deák, O. Valkó, A. Molnár V., B. Tóthmérész, P. Török, Do large-seeded herbs have a small range size? The seed mass–distribution range trade-off hypothesis. *Ecology and Evolution* **7**, 11204–11212 (2017).

26. M. H. DeSiervo, L. L. Sullivan, L. M. Kahan, E. W. Seabloom, L. G. Shoemaker, Disturbance alters transience but nutrients determine equilibria during grassland succession with multiple global change drivers. *Ecology Letters* **26**, 1132–1144 (2023).

27. A. Eskelinen, S. Harrison, Erosion of beta diversity under interacting global change impacts in a semi-arid grassland. *Journal of Ecology* **103**, 397–407 (2015).

28. R. S. Inouye, D. Tilman, Convergence and Divergence of Old-Field Vegetation After 11 yr of Nitrogen Addition. *Ecology* **76**, 1872–1887 (1995).

29. E. W. Seabloom, E. Batzer, J. M. Chase, W. Stanley Harpole, P. B. Adler, S. Bagchi, J. D. Bakker, I. C. Barrio, L. Biederman, E. H. Boughton, M. N. Bugalho, M. C. Caldeira, J. A. Catford, P. Daleo, N. Eisenhauer, A. Eskelinen, S. Haider, L. M. Hallett, I. Svala Jónsdóttir, K. Kimmel, M. Kuhlman, A. MacDougall, C. D. Molina, J. L. Moore, J. W. Morgan, R. Muthukrishnan, T. Ohlert, A. C. Risch, C. Roscher, M. Schütz, G. Sonnier, P. M. Tognetti, R. Virtanen, P. A. Wilfahrt, E. T. Borer, Species loss due to nutrient addition increases with spatial scale in global grasslands. *Ecology Letters* **24**, 2100–2112 (2021).

30. Q. Chen, S. Wang, E. W. Seabloom, A. S. MacDougall, E. T. Borer, J. D. Bakker, I. Donohue, J. M. H. Knops, J. W. Morgan, O. Carroll, M. Crawley, M. N. Bugalho, S. A. Power, A. Eskelinen, R. Virtanen, A. C. Risch, M. Schütz, C. Stevens, M. C. Caldeira, S. Bagchi, J. Alberti, Y. Hautier, Nutrients and herbivores impact grassland stability across spatial scales through different pathways. *Global Change Biology* **28**, 2678–2688 (2022).

31. Y. Zhang, J. Feng, M. Loreau, N. He, X. Han, L. Jiang, Nitrogen addition does not reduce the role of spatial asynchrony in stabilising grassland communities. *Ecology Letters* **22**, 563–571 (2019).

32. W. Lu, Y. Zhang, X. Chen, Z. Ren, H. Lu, R. Liu, Y. Zhang, Similar effects of seasonal nitrogen enrichment on plant species–area relationship in a temperate grassland. *Ecological Indicators* **158**, 111430 (2024).

33. D. R. Chalcraft, S. B. Cox, C. Clark, E. E. Cleland, K. N. Suding, E. Weiher, D. Pennington, Scale-dependent responses of plant biodiversity to nitrogen enrichment. *Ecology* **89**, 2165–2171 (2008).

34. B. L. Foster, E. J. Questad, C. D. Collins, C. A. Murphy, T. L. Dickson, V. H. Smith, Seed availability constrains plant species sorting along a soil fertility gradient. *Journal of Ecology* **99**, 473–481 (2011).

35. S. E. Koerner, M. L. Avolio, K. J. La Pierre, K. R. Wilcox, M. D. Smith, S. L. Collins, Nutrient additions cause divergence of tallgrass prairie plant communities resulting in loss of ecosystem stability. *Journal of Ecology* **104**, 1478–1487 (2016).

36. Z. Lan, G. D. Jenerette, S. Zhan, W. Li, S. Zheng, Y. Bai, Testing the scaling effects and mechanisms of N-induced biodiversity loss: evidence from a decade-long grassland experiment. *Journal of Ecology* **103**, 750–760 (2015).

37. Z. Xu, H. Ren, J. Cai, R. Wang, P. He, M.-H. Li, B. J. Lewis, X. Han, Y. Jiang, Antithetical effects of nitrogen and water availability on community similarity of semiarid grasslands: evidence from a nine-year manipulation experiment. *Plant Soil* **397**, 357–369 (2015).

38. X. Yang, G. Li, S. Li, Q. Xu, P. Wang, H. Song, D. Sun, M. Zhong, Z. Zhou, J. Song, J. Ru, S. Wan, L. Jiang, Resource addition drives taxonomic divergence and phylogenetic convergence of plant communities. *Journal of Ecology* **107**, 2121–2132 (2019).

39. X. Zhou, X. Liu, P. Zhang, Z. Guo, G. Du, Increased community compositional dissimilarity alleviates species loss following nutrient enrichment at large spatial scales. *Journal of Plant Ecology* **12**, 376–386 (2019).

40. R. H. Whittaker, Evolution and Measurement of Species Diversity. *Taxon* **21**, 213–251 (1972).

41. E. T. Borer, W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, M. D. Smith, Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution* **5**, 65–73 (2014).

42. J. M. Chase, B. J. McGill, D. J. McGlinn, F. May, S. A. Blowes, X. Xiao, T. M. Knight, O. Purschke, N. J. Gotelli, Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecology Letters* **21**, 1737–1751 (2018).

43. J. M. Chase, M. A. Leibold, Spatial scale dictates the productivity-biodiversity relationship. *Nature* **416**, 427–430 (2002).

44. E. W. Seabloom, E. T. Borer, Y. Buckley, E. E. Cleland, K. Davies, J. Firn, W. S. Harpole, Y. Hautier, E. Lind, A. Macdougall, J. L. Orrock, S. M. Prober, P. Adler, J. Alberti, T. Michael Anderson, J. D. Bakker, L. A. Biederman, D. Blumenthal, C. S. Brown, L. A. Brudvig, M. Caldeira, C. Chu, M. J. Crawley, P. Daleo, E. I. Damschen, C. M. D'Antonio, N. M. Decrappeo, C. R. Dickman, G. Du, P. A. Fay, P. Frater, D. S. Gruner, N. Hagenah, A. Hector, A. Helm, H. Hillebrand, K. S. Hofmockel, H. C. Humphries, O. Iribarne, V. L. Jin, A. Kay, K. P. Kirkman, J. A. Klein, J. M. H. Knops, K. J. La Pierre, L. M. Ladwig, J. G. Lambrinos, A. D. B. Leakey, Q. Li, W. Li, R. Mcculley, B. Melbourne, C. E. Mitchell, J. L. Moore, J. Morgan, B. Mortensen, L. R. O'Halloran, M. Pärtel, J. Pascual, D. A. Pyke, A. C. Risch, R. Salguero-Gómez, M. Sankaran, M. Schuetz, A. Simonsen, M. Smith, C. Stevens, L. Sullivan, G. M. Wardle, E. M. Wolkovich, P. D. Wragg, J. Wright, L. Yang, Predicting invasion in grassland ecosystems: Is exotic dominance the real embarrassment of richness? *Global Change Biology* **19**, 3677–3687 (2013).

45. P.-C. Bürkner, Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal* **10**, 395 (2018).

46. R Core Team., R: A language and environment for statistical computing., R Foundation for Statistical Computing. (2022).

47. T. M. Anderson, D. M. Griffith, J. B. Grace, E. M. Lind, P. B. Adler, L. A. Biederman, D. M. Blumenthal, P. Daleo, J. Firn, N. Hagenah, W. S. Harpole, A. S. MacDougall, R. L. McCulley, S. M. Prober, A. C. Risch, M. Sankaran, M. Schütz, E. W. Seabloom, C. J. Stevens, L. L.

Sullivan, P. D. Wragg, E. T. Borer, Herbivory and eutrophication mediate grassland plant nutrient responses across a global climatic gradient. *Ecology* **99**, 822–831 (2018).

48. E. T. Borer, W. S. Harpole, P. B. Adler, C. A. Arnillas, M. N. Bugalho, M. W. Cadotte, M. C. Caldeira, S. Campana, C. R. Dickman, T. L. Dickson, I. Donohue, A. Eskelinen, J. L. Firn, P. Graff, D. S. Gruner, R. W. Heckman, A. M. Koltz, K. J. Komatsu, L. S. Lannes, A. S. MacDougall, J. P. Martina, J. L. Moore, B. Mortensen, R. Ochoa-Hueso, H. Olde Venterink, S. A. Power, J. N. Price, A. C. Risch, M. Sankaran, M. Schütz, J. Sitters, C. J. Stevens, R. Virtanen, P. A. Wilfahrt, E. W. Seabloom, Nutrients cause grassland biomass to outpace herbivory. *Nature Communications* **11**, 1–8 (2020).

49. K. Van Sundert, M. A. S. Arfin Khan, S. Bharath, Y. M. Buckley, M. C. Caldeira, I. Donohue, M. Dubbert, A. Ebeling, N. Eisenhauer, A. Eskelinen, A. Finn, T. Gebauer, S. Haider, A. Hansart, A. Jentsch, A. Kübert, I. Nijs, C. A. Nock, C. Nogueira, A. J. Porath-Krause, D. Radujković, X. Raynaud, A. C. Risch, C. Roscher, M. Scherer-Lorenzen, M. A. Schuchardt, M. Schütz, J. Siebert, J. Sitters, M. Spohn, R. Virtanen, C. Werner, P. Wilfahrt, S. Vicca, Fertilized graminoids intensify negative drought effects on grassland productivity. *Global Change Biology* **27**, 2441–2457 (2021).

50. J. Lepš, 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 (2014).

Acknowledgments:
This work was generated using data from the Nutrient Network (http://www.nutnet.org) experiment, funded at the site-scale by individual researchers. We thank the Minnesota Supercomputer Institute for hosting project data and the Institute on the Environment for hosting Network meetings. We thank researchers from the NutNet who contributed data to our analysis, table S9 lists these researchers. We thank the Minnesota Supercomputing Institute for hosting project data and the Institute on the Environment for hosting Network meetings. Nitrogen fertilizer was donated to some NutNet sites by Crop Production Services, Loveland, CO. This experiment is funded by individual researchers at the site scale.
Funding: German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118-202548816) for the contribution of JMC, SAB, EL, QC, WSH, and other iDiv co-authors. ERC Advanced Grant (MetaChange) to JMC for the contribution of JMC, SAB. Views and opinions expressed are however those of the author(s) only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them.
National Science Foundation grant NSF-DEB-1042132 (ETB, EWS; for NutNet coordination and data management) National Science Foundation grant NSF-DEB-1234162 (ETB, EWS; for Long-Term Ecological Research at Cedar Creek). National Science Foundation grant NSFDEB-1831944 (ETB, EWS; for Long-Term Ecological Research at Cedar Creek), and the Institute on the Environment (DG-0001-13).

Author contributions:
Conceptualization: QC, JMC, SAB, EL, WSH; **Methodology**: QC, JMC, SAB; **Investigation and data collection**: all authors except QC, JMC, SAB, EL, EHG; **Visualization**: QC; **Writing—original draft**: QC; **Writing—review & editing**: all authors. See table S10 for more details for the contribution of each author.

Competing interests: Authors declare that they have no competing interests.

Data and materials availability: The NutNet data are publicly available on the Environmental Data Initiative (EDI) (https://doi.org/10.6073/pasta/583874460a0af70f93d 3eee2f22f9a13). The raw data used and processed data generated in this study and the R codes used to produce results in this study will be made publicly available once the manuscript is accepted.

Supplementary Materials

Materials and Methods

Figs. S1 to S23

Tables S1 to S10