1	Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems						
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43	The effects of biodiversity on ecosystem functioning generally increase over time but the underlying processes
44	remain unclear. Using 26 long-term grassland and forest experimental ecosystems we demonstrate that
45	biodiversity-ecosystem functioning relationships strengthen mainly by greater increases in functioning in
46	high-diversity communities in grasslands and forests. In grasslands, biodiversity effects also strengthen due to
47	decreases in functioning in low-diversity communities. Contrasting trends across grasslands are associated
48	with differences in soil characteristics.
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More than two decades of research have revealed that biodiversity is a significant driver of ecosystem functioning^{1,2}.
Positive biodiversity effects on ecosystem functioning have been found in grassland and forest biodiversity
experiments^{3,4} with growing evidence showing that biodiversity–ecosystem functioning relationships may become
stronger over time^{5,6,7}. Moreover, several recent studies suggest that long-term biodiversity effects in experiments
better mirror natural conditions than short-term studies and likely help explain biodiversity–ecosystem functioning
relationships in real-world ecosystems^{8,9,10,11}.

Temporal increases in plant diversity effects on ecosystem functioning may result from an increase in
functioning in high-diversity communities⁷, a decrease in functioning in low-diversity communities¹² or both.
However, it remains unknown which of the above trends drive temporal increases in diversity effects on ecosystem
functioning, whether these trends are consistent across experiments and ecosystems, and if not, whether contextdependency in temporal trends may be attributed to site conditions. For instance, soil characteristics likely influence
the biodiversity–ecosystem functioning relationship^{10,13,14} and may influence temporal trajectories as well, but
whether or not they do so is unclear.

Understanding temporal trends of biodiversity effects on ecosystem functioning is critical for providing insights into biodiversity–ecosystem functioning relationships^{9,16} and predicting the potential consequences that progressive biodiversity change^{18,19} and management^{20,21} have on ecosystem functioning and service provisioning over time. Further, examining these temporal trends is fundamental for guiding research on understanding the underlying mechanisms, e.g. a variety of niche-differentiation processes such as complementary resource use and facilitation, which can have positive effects on the functioning of high-diversity communities^{6,17}, and the impact of pest and diseases, which can have negative effects on the functioning of low-diversity communities⁹.

In this study, we examined temporal shifts in biodiversity effects on ecosystem functioning in terrestrial ecosystems, specifically plant diversity effects on plant aboveground biomass in grassland and on basal area in forest experimental ecosystems. We used data from 26 long-term biodiversity experiments that manipulated plantspecies richness in grasslands and forests (14 and 12 experiments, respectively; Supplementary Table 1). We investigated whether the strength of the biodiversity–ecosystem functioning relationship increases with time and whether temporal divergence across plant richness levels is driven by an increase in function in high-diversity communities, a decrease in function in low-diversity communities, or a combination of both. Finally, if temporal trends differed across experiments, we assessed the potential role of soil characteristics in shaping these temporaltrends.

94 In grasslands, the relationship between plant species richness and plant aboveground biomass was positive 95 and became significantly stronger over time (Supplementary Table 2, Fig. 1a). Temporal divergence across plant 96 richness levels was observed in 10 out of 14 grassland experiments (Supplementary Fig. 1). Although temporal 97 divergence was frequently associated with more diverse communities showing stronger increases in plant 98 aboveground biomass over time (Fig. 1a), the temporal increase of diversity effects was not determined by a 99 consistent trend across studies (see variance components in Supplementary Table 2): temporal divergence was 100 driven by a decrease in function in low-diversity communities in one experiment, by an increase in function in high-101 diversity communities in six experiments, or a combination of both in three experiments (Supplementary Fig. 1). 102 The context-dependency underlying biodiversity-ecosystem functioning relationships in grasslands was 103 strongly associated with variation in soil characteristics across experiments (Supplementary Table 3). Soils 104 influenced biodiversity-ecosystem functioning relationships in two ways. First, the interaction between soil 105 characteristics related to soil texture and pH and plant species richness shaped the overall richness effect (significant 106 richness × soil PC2 interaction; Supplementary Table 3 and Supplementary Figs. 2 and 3). Second, soil 107 characteristics, such as cation-exchange capacity (CEC), soil organic carbon (C), water content at wilting point, and 108 bulk density contributed to driving temporal divergence (significant richness \times time \times soil PC1 interaction; 109 Supplementary Table 3, Fig. 2, and Supplementary Fig. 2). Temporal divergence driven by an increase in function in 110 high-diversity communities was associated with studies located in areas with higher CEC, soil organic C, water 111 content, and lower bulk density, while a decrease in function in low-diversity communities was associated with the 112 inverse pattern, e.g. lower soil organic C (Fig. 2).

113 The general increase of the biodiversity–ecosystem functioning relationship through time was due to 114 contrasting trajectories across grassland studies, showing the importance of context-dependency of the biodiversity– 115 ecosystem functioning relationship in this ecosystem. Our analyses reveal that soil characteristics contribute to 116 strengthening plant species richness effects on ecosystem functioning in general¹³ and through time¹¹ in multiple 117 ways. First, variability in ecosystem functioning across plant species richness levels was generally lower in 118 experiments with sandy soils. Second, temporal divergence was explained by stronger increases in ecosystem 119 function in high-diversity than in low-diversity communities in experimental sites with higher soil organic C, 120 whereas temporal divergence in experimental sites with low soil organic C was explained by a decrease in 121 ecosystem function in low-diversity communities. Therefore, the influence of resource availability on plant-plant interactions as well as multi-trophic interactions¹⁹ may underlie temporal changes of biodiversity effects^{10,13} and 122 related mechanisms^{14,22}. It is also likely that other abiotic and biotic factors play a role in shaping the biodiversity– 123 124 ecosystem functioning relationship through time. For instance, most of the grassland biodiversity experiments are 125 perennial-dominated (more than 75% of the species were perennial), except for BIODEPTH Greece and Portugal 126 sites (less than 30% of the species were perennial), where there was no evidence of temporal divergence. Grassland 127 experiments dominated by annual plants may be strongly affected by processes related to recruitment, such as seed availability (either from their own plot or surrounding plots) and microsites²³. Recruitment may influence diversity 128 129 effects in grasslands, mainly due to changes in plant density rather than changes in plant size²⁴.

130 In forests, plant richness effects on periodic annual increment of basal area were consistently positive 131 across studies (see variance components in Supplementary Table 2, Fig. 1b, Supplementary Fig. 4), and, in contrast 132 to grasslands, we did not find evidence that they changed over time (neither time nor richness \times time were 133 significant; Supplementary Table 2, Fig. 1b). Consequently, the temporal divergence of total basal area among tree 134 species richness levels depended on consistently positive diversity effects on periodic annual increment of basal 135 area. (Supplementary Tables 2 and 4, Fig. 1c, and Supplementary Fig. 5). The absence of context-dependency in 136 forests could not be explained by overall differences in soil characteristics between forest and grassland studies, 137 which are located along similar soil gradients (Supplementary Figs. 6 and 7) that exhibit moderate differences in soil 138 cation-exchange capacity (p-value = 0.06) and pH (p-value = 0.02; Supplementary Fig. 8).

Our results show that positive tree diversity effects started early and accumulated through time. Thus, mechanisms associated with positive biodiversity effects on ecosystem functioning like complementarity may play a key role even during the early stages of community assembly²⁵. Decreases in ecosystem functioning in forests, e.g. due to tree mortality, appear to be offset by higher growth of surviving trees. This differs from grasslands, in which community-level biomass is highly dependent on plant density²⁴. Temporal divergence may continue to increase not only due to cumulative processes (detected in our study), but also due to strengthening of competitive interactions²⁶. The importance of niche partitioning over time also may increase at smaller spatial scales²⁷, and thus may require 146 longer to be detected at the plot level. Data availability from long-term studies and from more diverse forest systems 147 remain one of the main challenges for understanding temporal dynamics in forest experimental ecosystems. For 148 example, the longest-running forest biodiversity experiments in this study usually had communities with only one 149 and two species. Moreover, longer and multi-generation forest experiments may provide a better understanding of 150 the effects that pathogen and herbivore attacks and the accumulation of soil pathogens may have on biodiversity 151 effects through time. It is possible that temporal dynamics of biodiversity effects in forest ecosystems become 152 increasingly similar to those of grasslands when compared at similar stages in terms of generations of the study 153 organisms or under different soil characteristics, e.g. sites with lower CEC and higher pH (Supplementary Fig. 8).

154 In conclusion, our results show a consistent temporal divergence of ecosystem functioning across plant 155 diversity levels in both grassland and forest experimental ecosystems. In grasslands, temporal divergence was the 156 result of a variety of patterns, all ultimately causing an increase in biodiversity effects over time. In forests, by 157 contrast, temporal divergence was not detected when ecosystem functioning was measured as a rate (periodic annual 158 increment of basal area) but rather as an amount (total basal area). Therefore, the increasing strength of the 159 biodiversity-ecosystem functioning relationship in forests was related to an increase in function of high-diversity 160 communities driven by a consistent positive effect of high-diversity communities on periodic annual increment of 161 basal area. Temporal divergence in ecosystem functioning found in our analysis may have multiple implications for 162 the provisioning of vital ecosystem services in managed ecosystems. For instance, we need to determine other 163 potential biotic and abiotic factors that drive either an increase of ecosystem function in high-diversity communities 164 or a decrease in low-diversity communities over time. Such mechanistic understanding is fundamental as lowdiversity plant communities are widely used in productive landscapes^{20,21}. Overall, our results support the 165 166 importance of management practices that reinforce the functional and structural complexity of ecosystems at different spatial and temporal scales²⁰ and, crucially, either attenuate decreases in function in grasslands or increase 167 168 function in grassland and forest ecosystems.

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172 Methods

173 Data acquisition and description

174 Long-term experiments that have manipulated plant species richness in grasslands and forests were identified using 175 published meta-analyses, review papers on related topics and experimental platforms for biodiversity research 176 (Supplementary methods). Long-term experiments were included if: a) plant species richness was directly 177 manipulated through sowing or planting and included monocultures of all species present in the mixtures, b) raw 178 data at least at the plot level were available, c) aboveground plant biomass (in grassland) or basal area (in forest) 179 data from at least three points in time from different years were available, and d) the experiment was conducted for 180 at least 3 years in grasslands and 5 years in forests. For forests, the required experimental duration was higher than 181 for grasslands because the establishment of tree-dominated experimental studies and the biodiversity effects on 182 ecosystem functions are expected to take longer in forests.

183 Data from 26 long-term biodiversity experiments met these criteria (Supplementary Table 1) including 12 forest 184 experiments (370 plots, n = 1,887 measurements (plot by age combination) across experiments) and 14 grassland 185 experiments (1,045 plots, n = 7886 measurements (plot by age combination) across experiments). Annual peak 186 above ground biomass (g/m^2) and basal area (m^2/ha) were used in grassland and forests, respectively. In forests, we 187 included two types of ecosystem functions: - periodic annual increment of basal area - is a rate and is therefore 188 more comparable to annual peak aboveground biomass in grasslands (see Supplementary methods) and – total basal 189 area – is an amount that captures cumulative tree growth. Both measures were used to quantify ecosystem 190 functioning following the definition in Hooper³, i.e. ecosystem functioning includes ecosystem properties such as 191 process rates and the size of the compartments.

192 Temporal divergence

We used linear mixed-effect models to assess the temporal dynamics of ecosystem function among plant species richness levels using either plant aboveground biomass in grassland or basal area in forest experiments. We fitted a separate model for grassland experiments using annual peak aboveground biomass and two separate models for forest experiments, one using total basal area and the other using periodic annual increment of basal area. The initial model included plant species richness, time, and the interaction between richness and time as fixed effects in both 198 grassland and forest experiments. We then simplified models by excluding non-significant fixed effects and 199 interactions (p-value > 0.1). Plant richness was the sown or planted richness (natural logarithm), and time was 200 experimental age in years (natural logarithm). The natural logarithm transformation was used based on the 201 expectation of fast, initial increases in ecosystem function, followed by constant growth in the later years of the 202 experiment. Using a random slope and intercept structure, random effects were included for: study, study × richness, 203 study \times time, study \times richness \times time interaction, and a term for plot within study for grasslands and for total basal 204 area in forests. The random structure for periodic annual increment of basal area included study, study \times richness 205 interaction, and a term for plot within study. We accounted for repeated measurements within plots by using a first-206 order autoregressive covariance structure, which fitted the data better than a compound symmetry covariance 207 structure based on the Akaike information criterion. The best covariance structure was first-order autoregressive. 208 Models were fitted with asreml function in the asreml package in R, and the results were extracted using the 209 test.asreml function in the pascal package in R. Analyses were run in R version 3.2.4²⁹.

210 Effects of soil characteristics on temporal divergence

211 To explore the variation in temporal trends among grassland studies, an additional model was tested that included 212 species richness, time, soil characteristics, and their interactions (Supplementary methods). Because a consistent set of soil variables was not available across studies, we used data from SoilGrids250³⁰ to provide a general and 213 214 consistent description of the study area. However, these data are proxies for site-specific quantitative information 215 and need to be interpreted with caution. The soil characteristics were used to perform a principal component 216 analysis, in which the first and second axes explained 48 and 40% of the variation across grassland experiments, 217 respectively (Supplementary Fig. 2). We did not analyze the effects of soil characteristics in forest experiments 218 because we did not find evidence of multiple trends underlying the temporal divergence (Supplementary Table 2, 219 Fig. 1b). To compare the potential differences in the range of soil characteristics between experimental ecosystems, 220 we performed an additional principal component analysis including both forest and grassland studies 221 (Supplementary methods and Supplementary Figs. 6, 7, and 8).

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224	Data availability									
225	The data that support the findings of this study are available from the authors upon request.									
226	Code availability									
227	R code of linear mixed-effects models is provided in the Supplementary methods section.									
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229	References									
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273 Author contributions

- 274 N.E conceived the idea; N.E and N.G-R developed the idea; A.H, B.W, C.P, C.Pot, C.R, D.F, D.P, D.T, F.M, H.A,
- H.E, J.E, J.J, J.K, J.P. JvR, P.R contributed experimental data, N.G-R assembled the data; N.G-R and D.C analysed
- the data with the input from F.I, J.K, and A.H; N.G-R wrote the paper with substantial input from all authors.

277 Competing interests

278 The authors have no competing interests.

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289 Figures Legends

290 Figure 1. Ecosystem functioning in grassland and forest experimental ecosystems. In grasslands, trajectories of 291 aboveground biomass (g m⁻²) among plant species richness levels diverge over time (a). In forests, significant plant species richness effects on periodic annual increment of basal area $(m^2 ha^{-1})$ are consistent over time (b). The 292 293 consistent positive effect of high-diversity communities on periodic annual increment of basal area may explain the 294 temporal divergence in total basal area among plant species richness levels (c). For panels a and c, lines are mixed-295 effects model fits for each plant species richness level within each study (thin lines) or across all studies (thick 296 lines). For panel b, lines are mixed-effects model fits for each study (gray lines) or across studies (blue line). For 297 grasslands, above ground biomass was significant affected by species richness ($F_{1.5754,7} = 14.21$, p-value <0.001) and 298 the species richness \times time interaction (F_{1.5754.7} = 8.53, p-value <0.01). For forests, periodic annual increment of 299 basal area was significantly affected by species richness ($F_{1,1433,1} = 10.07$, p-value <0.01), and total basal area was 300 significantly affected by time ($F_{1,291,9} = 24.32$, p-value <0.001) and the species richness × time interaction ($F_{1,291,9} = 24.32$, p-value <0.001) 301 18.39, p-value <0.001). See extended information in Supplementary Tables 2 and 4. Data from 14 grassland (1,045 302 plots n = 7,886 measurements (plot by age combination)) and from 12 forest experimental ecosystems were entered 303 in the analyses (370 plots, n = 1,887 measurements (plot by age combination)).

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Figure 2. Influence of soil characteristics on temporal divergence in grasslands. Lines are mixed-effects model fits for each plant species richness level and soil characteristics within each study (thin lines) or across all studies (thick lines). Plots only show temporal trajectories of plant species richness levels present in at least two experimental grasslands. Soil characteristics are based on a principal component analysis; the first principal axis (Soil PC1) explained 48% of variation where positive values were associated with higher cation-exchange capacity, soil organic carbon content, and volumetric water content at wilting point and lower soil bulk density. See extended information in Supplementary Table 3 and Supplementary Fig. 2.



