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Locally rare species influence grassland ecosystem multifunctionality

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Species diversity promotes the delivery of multiple ecosystem functions (multifunctionality). However, the relative functional importance of rare and common species in driving the biodiversity–multifunctionality relationship remains unknown. We studied the relationship between the diversity of rare and common species (according to their local abundances and across nine different trophic groups), and multifunctionality indices derived from 14 ecosystem functions on 150 grasslands across a land-use intensity (LUI) gradient. The diversity of above- and below-ground rare species had opposite effects, with rare above-ground species being associated with high levels of multifunctionality, probably because their effects on different functions did not trade off against each other. Conversely, common species were only related to average, not high, levels of multifunctionality, and their functional effects declined with LUI. Apart from the community-level effects of diversity, we found significant positive associations between the abundance of individual species and multifunctionality in 6% of the species tested. Species-specific functional effects were best predicted by their response to LUI: species that declined in abundance with land use intensification were those associated with higher levels of multifunctionality. Our results highlight the importance of rare species for ecosystem multifunctionality and help guiding future conservation priorities.

1. Introduction

Many studies have demonstrated that high species diversity enhances ecosystem functioning both in experimental and natural assemblages ([1–4]; reviewed in [5] this issue). However, it has been argued elsewhere that it is not the total number of species *per se*, but the functional properties of the most locally abundant ones (hereafter common species) that drive ecosystem functioning (mass–ratio hypothesis [6]). Other work has shown that each common species can only provide a limited number of functions [1,7–8]. Extending the mass–ratio hypothesis to the simultaneous provision of multiple ecosystem functions at high levels (multifunctionality), we might, therefore, predict that several common species would be needed to maintain multifunctionality and that the diversity of common species, rather than overall

diversity, would be its main biotic driver. In contrast with this argument, less locally abundant (hereafter rare) species have been shown to play a crucial role in affecting several ecosystem functions [9–11]. Rare species comprise the vast majority of the species in any natural community and are more sensitive to anthropogenic disturbances [12,13]. Thus, quantifying the functional consequences of their loss is of particular importance to predict the provision of ecosystem services in the future. The functional importance of common versus rare species could depend on the ecosystem functions under scrutiny. Studies focused on productivity and pollination have found common species to be the main driver (e.g. [9,14–17]) while those focusing on functions associated with some regulating (e.g. invasion resistance) or recreational (e.g. birdwatching) services highlight the importance of rare species [18–20]. Owing to their contrasting effects depending on the function considered, studies measuring multifunctionality are required to comprehensively assess the relative functional importance of rare and common species [8,11].

Studies across large temporal or spatial scales have shown that the relationship between diversity and ecosystem functioning may change with abiotic conditions or land use intensification [21–25], the level of multifunctionality desired [8,26], or the type of organism being considered [23]. Land use intensification promotes shifts in the functional composition of multiple taxa (e.g. [27]), potentially dampening the generally positive relationship between diversity and ecosystem multifunctionality [25]. The effects of biodiversity might also depend on the level of multifunctionality considered [26,28]. High levels of many functions can be difficult to achieve if there are strong trade-offs between functions or between diversity effects on these functions. Finally, different components of biodiversity may differ in their functional effects. Above- and below-ground organisms differ in their sensitivity to climate or anthropogenic disturbances, with rare above-ground species being the most sensitive (e.g. [13,29]), and can also have different effects on ecosystem multifunctionality, with stronger effects found for above-ground organisms [23,30]. The context dependencies of the biodiversity–functioning relationship are poorly understood, particularly in terms of how they might modify effects of rare and common species. Existing comparisons of the functional role of rare versus common species have seldom been extended beyond single taxa, individual ecosystem functions, or a particular study site (but see [11]). In order to understand the response of natural and semi-natural ecosystems to ongoing global change, we therefore need to examine the relationships between different components of diversity (above- versus below-ground, common versus rare) and ecosystem multifunctionality across environmental gradients [23].

It has also been hypothesized that the presence of certain species can be of particular importance for ecosystem functioning, regardless of their abundance or whether they are above- or below-ground organisms (identity hypothesis [31,32]). This hypothesis has received empirical support from studies focusing on individual functions such as litter decomposition, parasitism or predation [33–35]. However, studies have not yet tested whether there are species that can drive overall ecosystem multifunctionality, which would require lack of trade-offs in their effects on different functions. If there are influential species, it is important to understand the characteristics that they possess and how they respond to land use intensification. If such species decline in abundance as land

use intensifies then, in addition to effects of biodiversity loss, compositional change driven by land use may have large effects on ecosystem multifunctionality.

Here, we assess the functional role of the diversity of rare and common species (based on their local abundance), both above- and below-ground, on several multifunctionality indices derived from 14 ecosystem functions, related to the delivery of supporting, provisioning, regulating and cultural services (*sensu* [36]). Our hypotheses are: (i) the diversity of common species is a more important driver of ecosystem multifunctionality than the diversity of rare species; (ii) the positive effect of diversity on multifunctionality will decline with land-use intensity (LUI) due to the associated changes in functional composition; (iii) the diversity of above-ground organisms is the strongest biotic predictor for ecosystem multifunctionality [23]; (iv) there are particular species, across multiple trophic levels, that can promote high multifunctionality, and land use intensification changes the abundance of these species.

2. Material and methods

(a) Study sites

We sampled 150 grassland plots (50 × 50 m) equally distributed over three regions across Germany: the UNESCO Biosphere Reserves Schwäbische Alb (located in the southwest) and Schorfheide-Chorin (in the northeast), and the area in and around the National Park Hainich-Dün (in central Germany; [37]). The 50 grassland plots per region were selected to span a gradient of the full range of land use practices and intensities found in Central European grasslands. Information about LUI was obtained directly from the land owners via questionnaires [37]. We used this information to calculate a compound measure of LUI which summarizes the three major components of land use in these grasslands—intensity of fertilization, mowing and grazing—with the following formula: $LUI = \sqrt{(F_i/F_R) + (M_i/M_R) + (G_i/G_R)}$, where F_i , M_i and G_i are the amount of fertilizer applied, frequency of mowing cuts and standardized units of livestock density within each sampling site per year, respectively. All three components were standardized by the average across the 50 grassland plots within each region (F_R , M_R and G_R ; see [38] for full methodological details). We averaged LUI across 2006–2010, the period when most diversity and functioning data were collected.

(b) Analyses at the community level

(i) Diversity measures

At each site, we measured the abundance and richness of nine trophic groups using standard methodology (see electronic supplementary material, table S1 for details). Overall, our sampling included approximately 4300 taxa (the taxonomic unit varied between groups, electronic supplementary material, table S1, but we refer to all as ‘species’, for simplicity). The groups were autotrophs (plants and bryophytes), below-ground herbivores (insect larvae), below-ground predators (insect larvae), detritivores (insects and millipedes), soil microbial decomposers (bacteria), above-ground herbivores (insects), above-ground predators (insects, spiders and centipedes), arbuscular mycorrhizal fungi and below-ground bacterivores (bacterivorous protists). Omnivorous arthropods were not considered in our analyses as there were too few of them.

Using data for each of these nine trophic groups we calculated multidiversity, i.e. a measure of overall diversity at the community level obtained by averaging standardized diversity measures across trophic groups [13]. To calculate multidiversity, we first classified the species into two groups according to their abundance (which

was measured differently for the various groups; electronic supplementary material, table S1): common (the top 10% of species in terms of total abundance) and rare species (the bottom 90% of species). Abundance is widely accepted as a measure of rarity (e.g. [39]); therefore, we chose abundance across all study sites to be the most representative measure of the overall rarity of our target species. The top 10% species (common species hereafter) accounted for 80% of the total abundance sampled, whereas the bottom 90% of species (rare species hereafter) made on average 20% of the total abundance (ranging from 6% in bacteria to 30% in below-ground herbivores; electronic supplementary material, figure S1). A second step in the calculation of our multidiversity metric was to standardize all variables to a common scale (between 0 and 1) by subtracting the minimum value and dividing by the maximum value found across the 150 sites to avoid the influence of different ranges in diversity characterizing each group. Third, we classified the trophic groups into above- and below-ground organisms (plants were considered above-ground organisms). Finally, we averaged their standardized values to obtain four measures of multidiversity: above- and below-ground common species multidiversity, and above- and below-ground rare species multidiversity.

(ii) Ecosystem function measures

At each site, we measured 14 different ecosystem functions. These were: above- and below-ground plant biomass, root decomposition rates, potential nitrification, soil phosphorus retention, arbuscular mycorrhizal fungal root colonization, stability of soil aggregates, soil organic carbon, forage quality, resistance to above-ground plant pathogens, above-ground pest control, pollinator abundance, bird diversity and flower cover (see [25] and electronic supplementary material, table S2 for detailed methodology). These ecosystem functions are related to nutrient cycling, food provision, sustainable soil use, pest resistance, or cultural and recreational services. We calculated three ecosystem multifunctionality metrics using these 14 functions and following the multiple threshold approach of Byrnes *et al.* [26], which sums up the number of measured functions that exceed a given threshold. These thresholds are defined as a given percentage of the maximum level found for each function, and we used three thresholds (50, 75 and 90%) to represent a wide spectrum. In order to reduce the influence of outliers, the maximum was defined as an average of the top five values for each function across our study sites.

(iii) Statistical analyses

We used multimodel inference based on information theory [40] to analyse the response of ecosystem multifunctionality to the multidiversity of above- and below-ground common and rare species. We performed a different analysis for each of the three multifunctionality metrics. Large-scale studies such as ours allow the quantifying of the relative importance of diversity regarding other drivers of ecosystem functioning, and the evaluation of changes in diversity–functioning relationships across contrasting environmental conditions. However, it is difficult from observational studies to infer causality as diversity–functioning relationships could be confounded by environmental factors affecting both diversity and ecosystem functioning. To avoid the latter, we controlled for factors that could affect both multidiversity and ecosystem functioning in our analyses; these were: study region, environmental variables (pH, soil depth and topography—an index based upon the position and steepness of each site, which is related to the accumulation of soil material and water availability [41,42]), and LUI. We removed elevation from the set of environmental predictors because it was highly correlated with soil depth (Spearman’s rank correlation, $\rho = -0.91$). We also accounted for potential context dependencies in the diversity–

multifunctionality relationship by including the interactions between LUI, region and the four multidiversity predictors.

To analyse the relative importance of environmental conditions, the multidiversity of above- and below-ground common and rare species, and the interactions between them, as drivers of ecosystem multifunctionality, we built a set of competing models including either: environmental variables only, environmental + diversity variables; or environmental + diversity variables and the interactions between diversity and region and/or LUI; see electronic supplementary material, table S3, for the full list of models). From these competing models, we selected those that best fitted our data according to the Akaike information criterion (AICc, corrected for small sample sizes). Thus, those models differing less than 2 AICc units from the most parsimonious model ($\Delta\text{AICc} < 2$) were included in the set of best-fitting models. We also calculated the importance of our different predictors as the sum of the AICc weights (a comparison with each model's AICc with the minimum AICc) of the models in which each predictor appears. To allow comparisons between main effects and interaction terms, we divided the importance of each predictor by the number of models in which it was included (16 for the diversity predictors (maximum importance 1/16), and 8 for their interactions with region and LUI (maximum importance 1/8); see [43] for a related approach).

As a sensitivity analysis, we repeated our multimodel selection but used the multidiversity of the bottom 50% of species, instead of the bottom 90%, as an alternative measure of rarity. These bottom 50% of species made up on average 3% of the total abundance (ranging from 0.04% in bacteria to 6% in below-ground herbivores; electronic supplementary material, figure S1 and table S4 for detailed results). We also repeated our analyses using the abundance, instead of the species richness, of above- and below-ground common and rare species (electronic supplementary material, table S5). Results of sensitivity analysis were broadly similar to the main ones and therefore are not further discussed.

(c) Analyses at the species level

(i) Selection of species

We selected a subset of individual species that occurred in all three study areas and in at least 10 of the 150 sites to obtain reliable parameter estimates (see *Estimation of the functional role of each species* below). Some of the trophic groups measured (detritivores, and below-ground herbivores and predators) were not included in these species-level analyses as they contained too few species fulfilling our selection criteria. Of those that did, soil microbial decomposers and bacterivorous protists were overrepresented. Thus, in order to obtain a balanced sampling size for each trophic group, we only selected the most and least abundant 25 species within each trophic group that met the criteria. These species roughly corresponded to those classified as common and rare in the community level analyses (electronic supplementary material, table S6). Thereby, we obtained a balanced sample size of 50 species per trophic group (approx. 50% of them common, approx. 50% rare), with the exception of above-ground predators, for which only 20 species met our criteria (270 species considered overall).

(ii) Estimation of the multifunctional role of each species

To estimate the multifunctional role of each species, we used the null-model approach of Gotelli *et al.* [44] as implemented by the software Impact [45]. This analysis allowed us to identify the presence of influential species, and whether or not the degree of functional influence was related to the average species' abundance, to their functional traits, or to their response to LUI. The latter allowed us to test for the effects of compositional changes, across trophic levels, driven by land use intensification on multifunctionality. This analysis further allows us to identify whether there are functional trade-offs within each trophic level; i.e.

whether some species within a group are significantly associated with multifunctionality. The null-model approach used performs linear regressions between the abundance of each species and a given function, and then compares the observed slope with 1000 random permutations of the values of the functional variable. From the randomizations, a standardized effect size (SES) for each species is calculated as: $\text{SES} = (S_{\text{obs}} - S_{\text{sim}})/\text{s.d.}$; where S_{obs} and S_{sim} are the observed and the average of the 1000 simulated regression slopes, respectively, and s.d. is the standardized deviation of the slopes obtained from these 1000 randomizations. SES values higher than 2 or lower than -2 show significant relationships between the abundance of a given species and the function used as a response. We used our three multifunctionality measures as a response and thus obtained three functional effect sizes for each of our target species (270 target species \times 3 multifunctionality scenarios = 810 comparisons). Owing to the increased type II error derived from multiple testing, 40 of these 810 comparisons would be expected to be significant only by chance; we found two times more significant results (electronic supplementary material, table S7), implying that our results were unlikely to be caused by multiple testing only.

By randomizing the functional variable instead of the species abundances, the null-model approach takes partially into account the structure of the biotic community (including species interactions and non-independent effects; see full discussion in [44]). However, this method is purely correlative and prone to confounding factors which could be driving both the function and the abundance of the target species. To control for the latter, we used the residuals of both the abundance of each species and the multifunctionality metrics after filtering for the same environmental variables used in the multimodel selection (region, LUI, soil pH and depth, elevation, and topography). Despite its limitations, this is to our knowledge the best method available to estimate the functional effects of many species (which would be logistically prohibitive to address experimentally).

(iii) Statistical analyses

We performed two complementary analyses at the species level. First, to assess the functional importance of above- and below-ground groups, and of rare and common species, we compared the number of significant positive and negative SES in each of the four categories of species, using Fisher's exact tests (better suited for low sample sizes than χ^2 analyses). This allowed us to assess if there are influential species related to multifunctionality, and if these are either common or rare, or mainly represented by above- or below-ground organisms. The second analysis aimed to understand further which features make a species influential for multifunctionality. To do this we performed multiple regressions with the SES of the functional effect of each species as a response variable, and the 'response to LUI' as a predictor. To correct for other species characteristics that might affect their multifunctional importance, we also included their average abundance (across all sites in which each species occurred) and functional traits (plant height and specific leaf area for plants, and body size for herbivores and predators; obtained from available databases [46,47]). 'Response to land use intensity' was the standardized coefficient of a linear regression between each species' abundance and LUI. The number of sites in which each species occurred (which was correlated also with the range in abundance values; $\rho = 0.45$) was introduced as covariate in our analyses as it could affect slope estimates in the null-model approach used. The traits selected are related to species responses to LUI [25,48,49] and also play an important role for ecosystem functioning [25,50]. Data on functional traits were not available for microbial decomposers, bacterivorous protists and symbionts. Context dependencies in the species-level analysis were accounted for by including the interaction between region, trophic group and abundance or response to LUI as extra predictors. The interactions with region were not

significant in any case and, therefore, they are not considered further. All analyses were performed using R v. 3.0.2 [51].

3. Results

(a) Community level

Between 10 and 18% of the variation in multifunctionality was explained by study region, environmental variables, LUI and our multidiversity metrics (figure 1). All the best models (those with $\Delta\text{AIC} < 2$) included at least one of the four multidiversity metrics, with models only including environment and LUI performing less well (ΔAIC between 2.6 and 7.1; electronic supplementary material, table S3). The effects of multidiversity on multifunctionality differed depending on the metrics considered. Above-ground multidiversity of common species was not significantly related to any of the multifunctionality measures, whereas the multidiversity of common species below ground was positively related to multifunctionality at the 50% of threshold, but not to the other multifunctionality measures (electronic supplementary material, table S3). The multidiversity of rare species both above and below ground was significantly, but oppositely (positive for above and negative for below ground), related to multifunctionality at the highest thresholds (75 and 90%; figures 1 and 2).

The relationships found between multidiversity (both above and below ground) and multifunctionality at the highest thresholds did not depend on LUI or study region (figure 1). The best models for both the 75 and 90% thresholds did not include interactions between region and/or LUI and multidiversity (electronic supplementary material, table S3). The best models for the 50% multifunctionality threshold, however, included interactions between region, and/or LUI, and one or more multidiversity metrics (figure 1; electronic supplementary material, table S3), thus demonstrating that multidiversity–multifunctionality relationships were context-dependent for the low threshold measure. Indeed, for multifunctionality at the 50% threshold the interactions were as important as the main effects (figure 1), and not including them increased the AICc by more than 3 units in all cases, suggesting a strong decline in model performance (electronic supplementary material, table S3). Interactions with region or LUI affected the associations between below-ground, but not above-ground, multidiversity and multifunctionality. The association between the multidiversity of below-ground common species and multifunctionality was positive in the southwest, neutral in the central region and negative in the northeast (see interaction coefficients in electronic supplementary material, figure S2). LUI also influenced the effect of below-ground multidiversity, with associations between the multidiversity of both rare and common species and multifunctionality becoming more positive with decreasing LUI (electronic supplementary material, figure S2). Regardless of the interactions with region and LUI, we found a higher importance of above-ground multidiversity for the 75% and 90% thresholds, which shifted towards a higher importance of below-ground multidiversity components at the 50% threshold (figure 1; electronic supplementary material, table S3).

(b) Species level

Apart from the community level effects of multidiversity, we found significant positive associations between the abundance

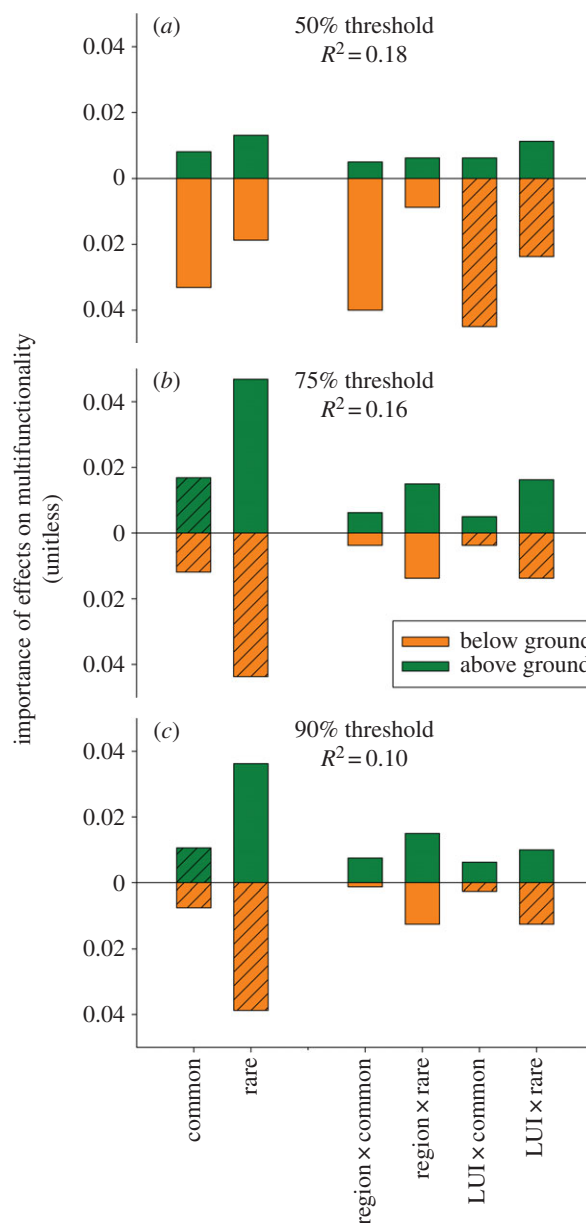


Figure 1. Importance of the different multifunctionality predictors as assessed by the sum of the AIC weights of the models in which each one was retained, divided by the number of models in which each variable was introduced. Green and brown indicate predictors associated with above- and below-ground multidiversity, which included the overall diversity of plants, bryophytes and herbivore, carnivore and decomposer arthropods (above-ground) and soil bacteria, bacterivore protists, arbuscular mycorrhizal fungi, and herbivore and carnivore insects (below-ground). Hatched bars indicate negative effects. Common = multidiversity of the top 10% most abundant species (80% of the individuals sampled), rare = multidiversity of the 90% least abundant species (20% of the individuals sampled). Region \times indicates the interaction term between study region and a given multidiversity metric. LUI \times indicates the interaction term between land use intensity and a given multidiversity metric. The R^2 of the best model for each multifunctionality metric (first row in electronic supplementary material, table S3) is provided.

of individual species and multifunctionality in 6% of the species tested, whereas we found negative relationships for 4% of the species (electronic supplementary material, table S7). Above-ground rare species had significantly more positive, and fewer negative, relationships with multifunctionality than the above-ground common species did (figure 3), a trend not found in below-ground organisms. The ratio between positive

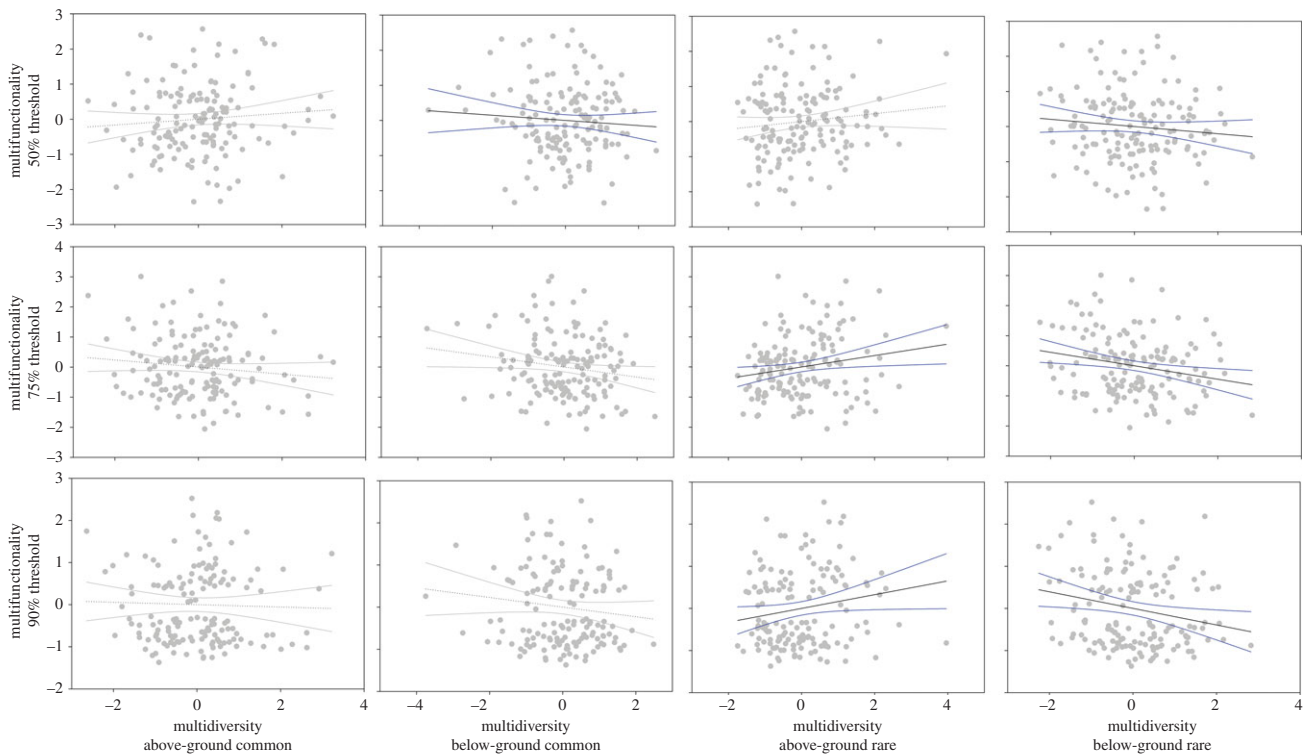


Figure 2. Effect of multidiversity of above- and below-ground, common and rare species on the different levels of multifunctionality. Slopes (with confidence intervals) were calculated after controlling for the other predictors in the model and are shown in blue if selected in the best models (see electronic supplementary material, table S3 and figure S2). Note that dots are residuals of both multidiversity and multifunctionality metrics after filtering by study region, LUI, soil pH and depth, and the topographic wetness index. (Online version in colour.)

and negative relationships differed substantially depending on the trophic group studied. Microbial decomposers had more positive than negative relationships with multifunctionality (11% versus 1%), with the opposite pattern observed in symbionts (4% versus 10%, electronic supplementary material, table S7). The remaining trophic groups showed slightly more positive than negative relationships.

Including the abundance, functional traits and response to LUI of the individual species allowed us to predict 13–16% of the variance in the strength of species–multifunctionality associations. The multiple regressions performed revealed that response to LUI was the strongest predictor of the associations between individual species abundance and multifunctionality. Species that increased in abundance in response to LUI were negatively correlated with multifunctionality at the 75 and 90% thresholds (figure 4; electronic supplementary material, table S8).

4. Discussion

(a) Effects of the multidiversity of rare and common species on multifunctionality

The important role that rare species play in maintaining individual ecosystem functions and, to some extent, multifunctionality has been highlighted previously [8,11,18–20]. Here, we extend those results to multitrophic assemblages in realistic landscapes, and show that (i) the relative importance of rare species increases when multifunctionality is defined using higher thresholds for the functions; and (ii) that this relationship remains relatively consistent across study regions and land use intensities (figure 2). Our results show that the ability of ecosystems to maintain a large number of functions at

average levels (50% threshold) is mainly driven by the diversity of common species and, intuitively, by the prevailing environmental conditions (as shown by the significant interactions found in our models). However, the delivery of a smaller number of functions, but at very high levels (75 and 90% thresholds), was mainly related to the multidiversity of rare species. The level of multifunctionality required will depend on stakeholder preferences, but the performance of many functions at their highest potential (high multifunctionality values at high thresholds) can be generally interpreted as a more desirable state of natural ecosystems. Overall, our study shows that the diversity of rare species is consistently and positively related to multifunctionality at the highest levels, thus implying the existence of ‘win-win’ scenarios between biodiversity conservation and ecosystem service provision.

A high diversity of rare species might be more beneficial for multifunctionality than a high diversity of common species if rare species are less likely to negatively affect ecosystem functions. We found that functional trade-offs between species, where some species have positive effects on multifunctionality and others negative effects, were less common among rare than among common species (figure 3). This could explain the stronger positive effect of rare species diversity on multifunctionality. Our correlative study does not allow us to investigate the mechanisms behind the lower incidence of such functional trade-offs in rare species. However, we speculate that if functional effects are driven by the presence of a given species, rather than by its abundance, they are much less likely to be negative. In the case of the presence-based functional effects, the species is either there and promotes a given function, or is absent and has no effect. For example, the presence of certain species can promote recreational services such as birdwatching [20], or prevent plant invasions [18,19]). Such presence-based effects are likely to be the dominant ones

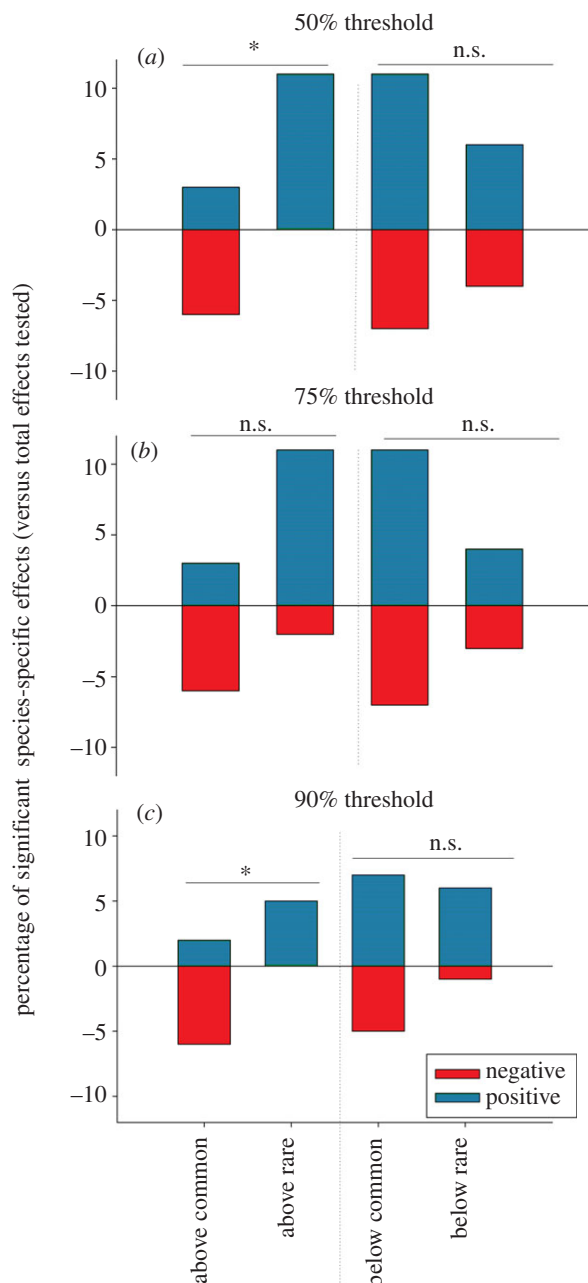


Figure 3. Summary of the relationships between individual species and multifunctionality. The percentage (according to the number of species tested) of significant positive (blue) and negative (red) effects are shown. The averaged results across each category (common versus rare species, above and below ground) are shown. Significant differences ($p < 0.05$) comparing the proportion of positive and negative effects in common and rare species according to Fisher's exact test are highlighted as $*$. n.s., not significant.

among rare species. By contrast, functional effects that are proportional to a species' abundance [6] may also be negative. Abundant species can reduce, rather than promote, a given function, e.g. species with low specific leaf area can reduce rates of nutrient cycling. Common species are more likely than rare species to have such abundance-related effects. Therefore, even if the common species are functionally relevant, they may have opposing functional effects (e.g. the positive effects of a common productive plant on forage production might be balanced by negative effects of a common herbivorous insect that feeds upon it). Such strong functional trade-offs between

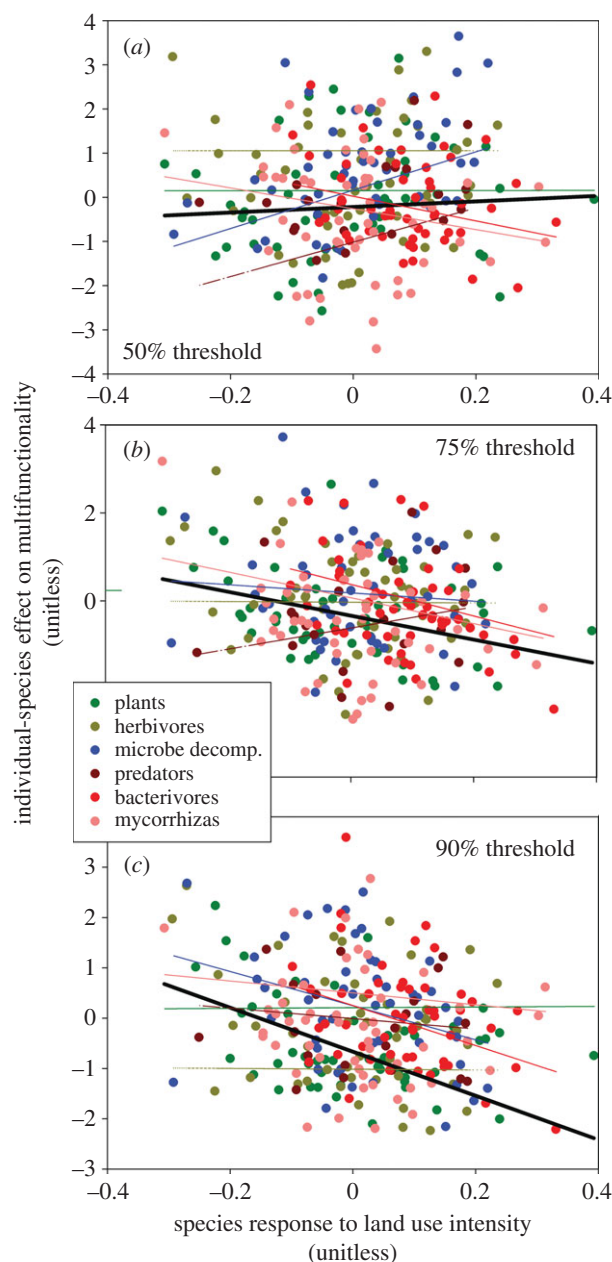


Figure 4. Relationship between the effect of each species (dots) on multifunctionality (standardized effect size) and its response to land use intensity (LUI). Different colours in dots and lines indicate the relationship found for each trophic group (slopes calculated after filtering by number of sites and average abundance). The black lines indicate the overall relationship (after filtering for the same factors and trophic group). Response to LUI was measured as the standardized slope of a regression between LUI and the abundance of each species.

common species could therefore result in a small effect of common species diversity on multifunctionality and a greater importance of rare species diversity in promoting multifunctionality. A complementary explanation for the higher functional importance of rare species is that they tend to be less redundant than common species in the functional traits they possess and, therefore, support communities with more distinct combinations of functional traits [52]. This enhanced functional diversity could also explain the positive functional effect of the multidiversity of rare species, as functional diversity is related to the provision and stability of multiple ecosystem functions [53,54].

While our study provides unique insights regarding the role of community level diversity on the provision of multiple

functions simultaneously, the use of these aggregate metrics obscures detailed information regarding the relationships between specific taxa and functions. A full description of such functions is outside the scope of this study but could partially explain the relatively low R^2 of our models (less than 0.20%; see [55] for a full discussion on the topic). The trade-offs we observed in the functional effects of common species would, obviously, not apply when studying ecosystem functions in isolation. Another reason for the relatively low proportion of explained variance could be the influence of factors operating at large spatial (i.e. surrounding landscape) and temporal scales (i.e. legacy effects of past land uses), which were not considered in this study [56].

(b) On the functional role of above- versus below-ground multidiversity

Below- and above-ground biotic components are known to respond differently to anthropogenic disturbances and are likely to differ in their effects on ecosystem functioning (e.g. [13,30]); however, very few studies have explored their separate functional roles [23]. We found that above-ground multidiversity, particularly of rare species, was often positively related to multifunctionality at the highest levels, whereas below-ground multidiversity was negatively associated with it. Above-ground rare species are highly sensitive to anthropogenic disturbances [13,29] and these findings suggest that they are also amongst the most functionally important species. Our results support the crucial role of the diversity of above-ground organisms, e.g. plants [1–4,8], but also herbivores [28] or predators [57], in determining ecosystem multifunctionality.

The stronger positive relationship between above-ground compared to below-ground diversity with multifunctionality concurs with the only previous study including these two groups separately [23]. It may be argued that the higher importance of above- compared to below-ground components is dictated by the selection of ecosystem functions studied; however, this is unlikely as both our study and Jing *et al.* [23] included a high proportion of soil-related variables. It seems that, when considered alone, below-ground diversity explains variation in multifunctionality that could be mainly due to its correlation with above-ground diversity [23,57], but further studies are required to test whether the pattern we observed holds across a wide variety of ecosystems and environments. Importantly, our snapshot sampling design may have reduced our capacity to compare the effects of both above- and below-ground multidiversity, as below-ground organisms are less sensitive to anthropogenic disturbances [13] and thus they could increase stability in ecosystem functioning by increasing response diversity [58].

The negative relationship between below-ground diversity and ecosystem multifunctionality, however, is surprising and contrasts with previous research (e.g. [23,59,60]). Soil biota effects are often driven more by functional composition than by species richness *per se* (see [59] for a review). Hence, the negative relationship between below-ground multidiversity and ecosystem functioning could reflect compositional changes rather than diversity effects [23,24]. Another potential explanation for these results is that the functional effects of below-ground diversity are context-dependent and change with climate or soil (regional differences in our study sites [61]), or with land use intensification (electronic supplementary material, figure S2; see also [23]). The latter could obscure the

overall effect of below-ground multidiversity on ecosystem functioning when it is investigated across wide environmental gradients. In this regard, we found strong context dependency for low (50%) levels of multifunctionality, as the relationship between below-ground multidiversity and multifunctionality changed both with study region and LUI (electronic supplementary material, figure S2). Regardless of the underlying mechanisms, the contrasting relationships between above- and below-ground biotic components and multifunctionality highlight the necessity to consider both in order to better understand the functional consequences of biodiversity loss in realistic landscapes.

(c) Individual species' effects on multifunctionality

Substantial research effort has been devoted to explain the functional role of individual species in natural ecosystems. Previous research suggests that the most abundant species [6], or a few key species with particular functional traits [31], will have the strongest effect on ecosystem functioning. These two hypotheses have received substantial empirical support across a large variety of systems and individual functions [6,14,15,17,32–35], but have rarely been tested for multiple functions simultaneously, or across multiple trophic groups. In addition to the effects of the diversity of the entire community, for 10% of the species tested, we found a significant relationship between their abundances and multifunctionality. This suggests that, despite potentially contrasting functional effects (positive, negative or neutral, depending on the function), some species, even individually, influence the overall ability of ecosystems to simultaneously provide multiple functions. This result supports the identity hypothesis [31,32], extending it to multiple functions and trophic levels. An example of one of these particularly influential species is *Hieracium pilosella*, a plant native to central Europe and locally rare in our study sites. This species was positively associated with multifunctionality according to our method and has previously been shown to increase soil organic carbon, litter decomposition and microbial biomass in comparison to other grassland species [62], to attract a variety of pollinators [63] and to have a relatively high resistance to pathogenic fungal infections [64]. We found a similar number of influential species for both common and rare species, and for both above- and below-ground organisms; indicating that individual species within these biotic components are equally important for multifunctionality. Understanding the attributes of these particularly influential species and their effects on multifunctionality should be a research priority if we are to predict the consequences of biodiversity loss and compositional changes for ecosystem service provision.

The direction of the relationship between the abundance of individual species and multifunctionality was best predicted by the response of individual species to land use intensification, even after accounting for the range in abundance across the plots and important functional traits. Previous studies have shown that land use intensification shifts plant functional composition and leads to an increase in the abundance of productive species, which enhance some provisioning services but compromise regulating and cultural services such as carbon storage or aesthetic value, therefore, reducing overall multifunctionality [25]. Similarly, changes in the ratio between soil fungi and bacteria with land use intensification may speed up nutrient recycling but

reduce ecosystem recovery after disturbances [24]. We show here that, alongside reducing their diversity, land use intensification may substantially influence the effect of multiple trophic levels, via compositional changes, on ecosystem functioning. Our results, therefore, suggest that the negative effect of LUI on multifunctionality at high thresholds could be, at least partly, caused indirectly by the negative response of particularly influential species to land use intensification. Such compositional changes might be particularly relevant for below-ground communities, whose relationships with multifunctionality (50% threshold) became negative under increasing LUI (electronic supplementary material, figure S2).

5. Conclusion

Substantial research effort has raised awareness of the functional consequences of losing biodiversity. However, we are still far from fully understanding which species or biodiversity attributes conservation efforts should focus on if ecosystem services are to be conserved. Our results suggest that locally rare above-ground species are the most important diversity component to preserve high levels of ecosystem multifunctionality in managed grasslands, perhaps due to their lower proportion of negative functional effects. Our multitrophic approach also supports the identity hypothesis, and extends it to multiple trophic groups and functions by showing, for the first time, that approximately 10% of the

species tested can be particularly associated with overall ecosystem functioning. We also found that the effect of an individual species on multifunctionality is related to its response to LUI, which will help to anticipate the functional consequences of compositional changes across multiple trophic groups caused by land use intensification.

Authors' contributions. S.S. and E.A. conceived the study, all the authors but S.S. and E.A. gathered the data, M.G. compiled the trait data, S.S. and E.A. did the analyses, S.S. wrote the first draft and all co-authors significantly contributed to improve it.

Competing interests. We declare we have no competing interests.

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